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SYSTEMATICS AND EVOLUTION OF THE GREATER ANTILLEAN HYLID FROGS

By

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The origins and number of ancestral stocks of the hylid fauna of the West Indies have been debated. The twelve species are now allocated to the genus *Hyla*. The Lesser Antillean treefrog fauna is depauperate, consisting only of a member of the *Hyla rubra* complex which occurs on the island of Saint Lucia. The occurrence of this small hylid on only one of the islands in the Lesser Antilles is puzzling, unless *Hyla rubra* is a relatively recent immigrant or adventive from the South American fauna, as seems probable. The species (or closely related members of the species group) is present on the continental islands of Trinidad and Tobago and is widespread on mainland South America. *Hyla squirella* has been introduced to Grand Bahama (Crombie, 1972), and *Hyla cinerea* is an apparent adventive to Puerto Rico (Albert Schwartz, pers. com.); both are common in the southeastern United States. Eight of the remaining species are endemic to either Jamaica or Hispaniola, and the ninth species is rather widespread; it occurs on Cuba and the Isle of Pines, the Bahamas, and southern peninsular Florida and recently has been introduced to Puerto Rico. Unlike *Hyla rubra* of the Lesser Antilles, *H. cinerea* of Puerto Rico, and *H. squirella* of Grand Bahama in the aforementioned nine species, there are no immediately obvious affinities between these Greater Antillean species and mainland representatives. The systematic relationships among the nine

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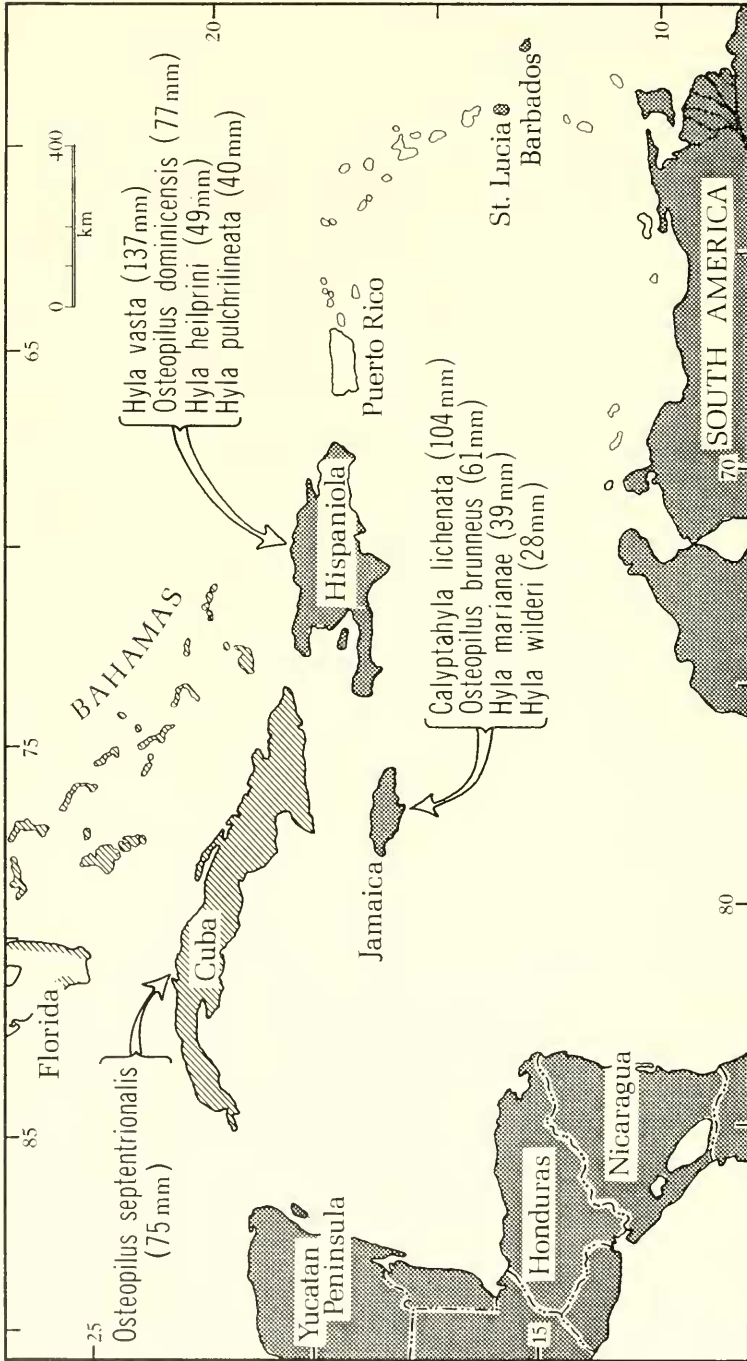
Fig. 1. Map of the West Indies showing distribution of resident hylid fauna of Greater Antilles. Distribution of *Osteopilus septentrionalis* is indicated by cross-hatching. Parenthetical numbers are average sizes of adult female frogs.

species themselves remain obscure, although they have received considerable attention in the past from Dunn and Noble, among others.

Our interest in these frogs is an outgrowth of several other morphological and systematic studies, which, in one way or another, have involved this isolated group of anurans. Because of the availability of specimens, *Hyla septentrionalis* was used by Trueb (1966) to describe the histology and development of exostosis, casquing, and integumentary-cranial co-ossification. Although the results of this research subsequently proved to be extremely useful in systematic considerations of other casque-headed, co-ossified hylids (Trueb, 1970), little was learned about the relationships of the casque-headed hylids of the Greater Antilles (*Hyla septentrionalis, H. brunea, H. dominicensis,* and *H. lichenata*). As a part of his larger study of the vocal sac structure in hylids, Tyler (1971) noted the occurrence of a unique type of throat musculature in three of the Greater Antillean frogs—*septentrionalis, brunnea,* and *dominicensis.* The accumulated morphological evidence suggested that the nine resident frogs were not so closely related as previously proposed by Dunn (1926), and prompted us to undertake this review of the taxa.

The format of the following review has been dictated by the peculiarities of the problem and our own limitations. Regrettably, neither of us has been able to observe any of these species in their natural habitat. In order to provide a general understanding of the distributions of the Greater Antillean hylids and the kinds of habitat available to them, we have provided cursory statements of the major topographical and phytogeographical features of the Greater Antilles and Bahamas. Because few species are involved, we elected to compare and contrast each of the nine species with respect to various morphological features of adults and larvae, and characteristics of breeding. The analysis of characters includes information from the literature and much new osteological and myological data. Together, these data provide a base for the critical reinterpretation of the systematics, evolution, and zoogeographic history of the Greater Antillean hylid fauna.

Acknowledgments

Materials and Methods

Measurements (Tables 1 and 2) and descriptions of external morphological features are based on examination of 140 preserved specimens. Myological observations were made on 27 preserved specimens, and osteological descriptions are based on 31 skeletal preparations.

The majority of characters analyzed are used commonly and require no special explanation other than that provided in text, and in text references. In the section dealing with osteology, several characters are discussed which should be clarified. The first group of these involve the structure of the vertebral column (Fig. 2A and B). The widths of presacral vertebrae and the sacrum were determined by measuring the linear distance between the distal tips of the transverse processes to the nearest 0.1 mm with dial calipers (Fig. 2A). Such measurements are not an index to the actual length of the transverse processes; we have gauged the overall dimension of individual vertebrae without accounting for the orientation of the transverse processes. The resulting values are useful in generating a profile of vertebral shape and only of limited use in comparing individual vertebral elements (e. g., width of presacral III and sacrum). The anterior sacral angle (Fig. 2B) was determined by measuring the angle between the longitudinal axis of the vertebral column and the leading edge of the sacral diapophysis. The posterior sacral angle is that angle between the longitudinal axis and the posterior edge of the diapophysis. Sacral diapophysis expansion can be calculated by subtracting the sum of anterior and posterior angles from 180°. Camera lucida drawings of the vertebral columns were made, and the angles were measured with a protractor from these drawings.

Two characters are of particular interest in the pelvis (Fig. 2C). The first of these, relative ilial length, was determined by measuring the greatest length of the ilium and the length of the acetabular portion of the pelvis—*i.e.*, the distance from the preacetabular margin of the ilium to the posterior margin of the ischium. The pelvic angle is that angle, in lateral profile, between the acetabular
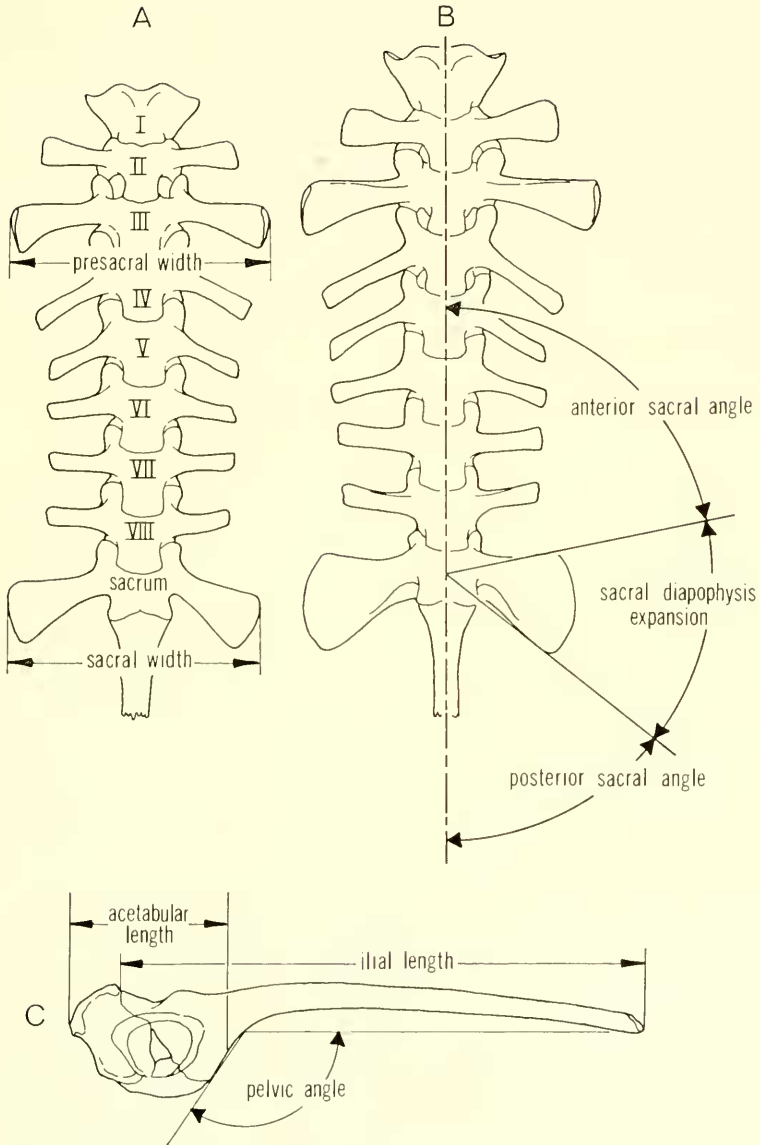
Fig. 2. Graphical explanation of postcranial osteological measurements. A. Ventral view of vertebral column of *Hyla vasta*. B. Ventral view of vertebral column of *Osteopilus brunneus*. C. Lateral aspect of pelvic girdle of *Osteopilus septentrionalis*.

portion of the ilium and the horizontal plane of the ilial shaft. In all cases, the values assigned this character are visual estimates—acute, nearly 90°, or obtuse.

Of the myological characters, the extrinsic musculature of the cloaca requires explanation here because these muscles previously have not been employed in anuran systematics. In fact, attention to the cloaca hitherto has been confined to descriptions of the musculature in such aberrant genera as *Ascaphus* (Du Toit, 1955) and *Rhinophrynus* (Noble, 1922).

The nomenclature that we adopt (see Fig. 3) differs from that of previous authors. The most proximal muscle, for which we propose the name *Musculus ischeococcygeus* is the *M. compressor cloacae* of Noble (1922) and some previous authors. We propose
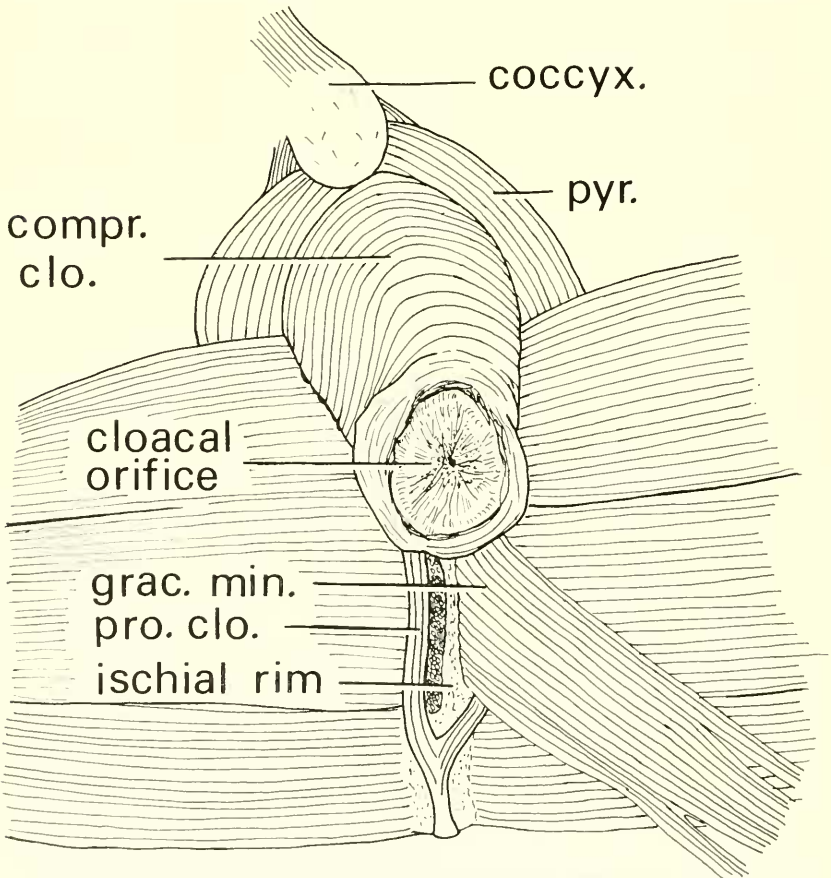

FIG. 3. Posterior aspect of thighs of *Osteopilus septentrionalis*. Superficial portion of *M. gracilis minor* removed from left side. Abbreviations: *compr. clo.*, *M. compressor cloacae*; *grac. min.*, *M. gracilis minor*; *pro. clo.*, *M. protractor cloacae*; *pyr.*, *M. pyriforms*.

this new name because this muscle occupies a pre-cloacal position and does not in any way compress the cloaca. The adjacent muscle is a genuine cloacal compressor and our use of compressor cloacae for it is in agreement with the actions of Du Toit (1955). A previously unreported muscle which we find occurs in many hylid species we name the *M. protractor cloacae.*

Studies of musculature were assisted by the use of iodine/potassium iodide staining technique described by Bock and Shear (1972).

We express the vocal sac aperture as a fraction of the mandible length. This was obtained from the maximal diameter of the vocal sac aperture (usually on a longitudinal axis), and the distance between the mandibular symphysis and the postarticular extremity of the mandible.

DISTRIBUTION OF THE GREATER ANTILLEAN HYLID FAUNA

At the risk of over-simplification, the Greater Antilles and Bahama Islands may be subdivided arbitrarily into five geographical subunits according to the distributions of the resident treefrogs (Fig. 1). These are: 1) Jamaica, 2) Hispaniola (Haiti and the Dominican Republic), 3) Cuba and the Isle of Pines, 4) the Bahama Islands, and 5) Puerto Rico. The following accounts are extremely brief and simplified, and intended only to introduce the reader to the habits, habitats, and distributions of the resident treefrogs. We also hope these accounts will serve as a modest, if superficial, summary of the principal topographical and vegetational features of the geographical subunits. Information on the latter was derived from inspection of a variety of topographic and vegetation maps and the accounts of Verdoorn (1945), and Rabb and Hayden (1957).

It is important to note that all the islands of the Greater Antilles are very diverse ecologically, each ranging from arid lowland deserts to high, upland deciduous or pine forests. The islands differ principally in their physiographic complexity. Hispaniola is the most complex (see Schwartz, 1973), whereas Puerto Rico and Jamaica are smaller and more simple. Each of these islands consists mainly of a central mountain mass surrounded by lowlands. In contrast to Jamaica and Puerto Rico, the largest island, Cuba, is characterized by three isolated mountain masses with surrounding lowlands.

Jamaica.—The four endemic hylids which occur on this relatively small island (*ca.* 224 x 80 km) are *Hyla lichenata, H. brunnea, H. marianae,* and *H. wilderi.* Topographically, the island is diverse. It is bisected longitudinally by a highland mass, the peaks of which lie between elevations of 1500 and 2100 m. The western and central three-fourths of the island comprise a plateau reaching elevations of 900 m. On the southern margin of Jamaica, there is

an irregular coastal plain (maximally 24 km in width). A typically insular climate prevails, with the northeast sector receiving the highest annual precipitation, the central plateau somewhat less, and the southern coastal plain the least. The dry coastal plain is characterized by cactus, thorn bush, and dry scrub. In contrast, the northern aspect of the island is heavily wooded, with tropical rainforest on the more remote slopes. The southern aspect of the island supports a drier, sclerophyllous vegetation consisting of park-savanna with scattered palms, pines, and scrub. The extensive central plateau is thickly wooded on its northern side and at higher elevations. Parkland and pasturage characterize lower elevations. The central and southern parts of the plateau are cultivated.

Hyla brunnea is the most widespread of the four species; it occurs over almost the entire island at elevations below 1500 m (Schwartz and Fowler, 1973). This moderately large, casque-headed frog (adults attain 76 mm snout-vent length; Schwartz and Fowler, 1973) is found most often in arboreal and terrestrial bromeliads in open woods. *Hyla wilderi* seems to be widely distributed over the central plateau at elevations between 122 and 610 m (*op. cit.*). This species is small (adults reach about 30 mm snout-vent length) and is not casque-headed; it occurs sympatrically with *brunnea* and frequents arboreal and terrestrial bromeliads in open woods. *Hyla lichenata* is the largest (adults reaching 122 mm snout-vent length; Gosse, 1851) of the four species and is distinguished by its rugose patterned, casqued cranium. Although documentation is poor, the frog seems to be rather widely distributed throughout most of the island at low to moderately high elevations. In contrast to *brunnea* and *wilderi, lichenata* is reported to be an inhabitant of more densely wooded forests, where it has been observed to perch in hollows in branches 1.2 to 3.6 m above the ground (Dunn, 1926). *Hyla marianae* is moderately small (adults reaching 39 mm snout-vent length) and inhabits bromeliads in dense and scattered deciduous forests between elevations of 122 and 895 m (Schwartz and Fowler, 1973). It is at least partially sympatric with each of the three other species. All four species deposit their eggs exclusively in the water-filled leaf bases of bromeliads. Although they have been reported to inhabit both terrestrial and arboreal bromeliads, eggs have been found only in arboreal bromeliads. Apparently, none of the species occurs on the xeric, southern coastal plain.

Hispaniola.—Although Hispaniola is larger (*ca.* 640 x 288 km) and more diverse topographically and vegetationally than Jamaica, again, only four species of hylids occur on the island—*Hyla dominicensis, H. vasta, H. heilprini,* and *H. pulchrilineata;* all are endemic. Hispaniola is the second largest Antillean island and probably the most complex physiographically. There is a central east-to-west mountain mass, the highest peak of which lies at an

elevation of 3175 m. The mountains are fragmented into a number of spurs and parallel chains. At higher elevations, the mountains support a mixed pine and broadleaf forest. Extensive areas of tropical rainforest occur at lower elevations in the central, northeastern and eastern portions of the island, whereas the peripheral, low elevations and coastal plains are characterized by park-savanna with palms and scrub. Xeric lowland dry scrub associations exist along the northwestern coast and south-central coastal areas.

Apparently, *Hyla dominicensis* is the most common and widespread of the resident hylids. The distribution of this relatively large frog (adults attain 99 mm snout-vent length) seems to be island-wide from the coastal lowlands to moderate elevations in the foothills. The species is principally an inhabitant of parkland-savanna and tropical rainforest environments. It is known to deposit its eggs in stagnant pools of rainwater in the forest and along the edge of stream banks (Noble, 1927). The second large treefrog of Hispaniola is *Hyla vasta* (adults reach 137 mm in snout-vent length). This non-casque-headed species is considerably scarcer in collections than *dominicensis* and perhaps, therefore, less common. It occurs sympatrically with *dominicensis* at moderate to low elevations and has been observed to lay its eggs in small gravel and stone depressions in quiet pools along streams (Noble, 1927). Schwartz (pers. com.) indicated that *vasta* is also partially sympatric with *Hyla heilprini* which breeds in torrenial streams. *Hyla pulchrilineata* is the smallest member of the Hispaniolan hylid fauna. Adults attain a snout-vent length of 43 mm, and the cranium bears no dermal modifications. Published locality records for this species are scarce, but Schwartz (pers. com.) indicated that *pulchrilineata* is widespread on the island, occurring from the coastal lowlands to an elevation of about 636 m; thus, *pulchrilineata* seems to be sympatric with *dominicensis*, *vasta*, and *heilprini*. Nothing has been reported concerning the larvae and reproductive behavior of this species. The fourth species, *Hyla heilprini*, is moderate in size (adults reaching 54 mm snout-vent length) and lacks cranial ornamentation. The limited locality records for this frog indicate that it inhabits the central Hispaniolan highlands; however Schwartz (pers. com.) reported that the species is more widespread than suggested in the literature and implied that *heilprini* is not limited to the highlands. Noble (1927) reported that *heilprini* was found along streams at places where the water fell in cascades over rocks.

Cuba and the Isle of Pines.—Cuba, the largest of the Antillean islands, and its small insular associate, the Isle of Pines, have only one treefrog, the moderately large (adults up to about 75 mm snout-vent length), casque-headed *Hyla septentrionalis*. In contrast to the other Greater Antillean treefrogs, this species is not endemic to a single island; it occurs in the Bahamas, southern

TABLE 1. Tabulation of means and ranges of body sizes and proportions of smaller members of the Greater Antillean hylid fauna. Abbreviations: HL, head length; HW, head width; IOD, interorbital distance; SVL, snout-vent length; TIB, tibia length; and TYMP, tympanum diameter.

Species	SVL (mm)	Tib/SVL (%)	HL/SVL (%)	HW/SVL (%)	IOD/HW (%)	Tymp/Eye (%)
Hyla pulchrilineata						
♂ (N=20)	31.6 (28.7-39.5)	50.5 (46.3-54.1)	34.2 (32.2-36.0)	32.0 (30.3-34.2)	29.4 (27.8-31.0)	61.6 (54.8-67.6)
♀ (N=6)	40.1 (37.6-42.8)	50.8 (48.4-53.0)	33.4 (31.7-35.1)	32.0 (31.2-32.6)	29.7 (27.4-31.1)	57.3 (48.9-62.8)
Hyla heilprini						
♂ (N=12)	49.4 (47.0-54.3)	53.1 (49.1-57.0)	35.7 (33.9-37.6)	35.9 (34.0-38.4)	28.2 (23.4-30.6)	59.9 (55.5-65.3)
♀ (N=4)	49.3 (46.2-52.0)	51.5 (49.6-53.7)	35.0 (33.9-36.4)	36.2 (34.5-37.2)	28.1 (26.9-28.8)	53.4 (51.7-56.6)
Hyla marianae						
♂ (N=3)	28.0 (23.4-33.1)	52.8 (51.3-53.8)	38.0 (36.9-38.9)	38.0 (34.2-37.9)	33.8 (33.3-34.1)	50.5 (47.1-52.6)
♀ (N=2)	38.7 (37.7-39.6)	51.3 (50.1-52.5)	36.2 (35.3-37.1)	36.0 (37.6-38.4)	30.8 (30.7-31.0)	50.4 (47.5-53.3)
Hyla wilderi						
♂ (N=15)	25.8 (23.8-27.3)	52.6 (49.2-55.8)	34.4 (31.7-36.0)	35.8 (34.1-37.5)	32.3 (28.7-37.8)	51.5 (46.4-56.0)
♀ (N=7)	27.3 (25.4-28.7)	52.1 (50.2-54.0)	33.4 (32.1-34.1)	35.1 (34.5-35.6)	32.2 (31.3-33.0)	52.5 (50.0-54.5)

TABLE 2. Tabulation of means and ranges of body sizes and proportions of larger members of the Greater Antillian hylid fauna. Figures marked by asterisks represent means of a sample of two. In those instances in which ranges are absent, the means are based on a literature report in which ranges were not provided (Duellman and Schwartz, 1958). See table 1 for abbreviations.

Species	SVL (mm)	Tib/SVL (%)	HL/SVL (%)	HW/SVL (%)	IOD/HW (%)	Tymp/Eye (%)
Osteopilus brunneus						
♂ (N=6)	45.5 (41.0-48.1)	47.3 (45.1-51.8)	37.3 (36.2-39.0)	36.8 (35.4-38.1)	39.4 (32.8-45.0)	71.9 (63.6-76.8)
♀ (N=6)	60.5 (52.5-70.0)	46.7 (44.7-49.1)	35.6 (33.0-38.4)	35.6 (33.7-38.1)	43.8 (40.5-46.6)	75.5 (72.7-80.6)
Osteopilus dominicensis						
♂ (N=20)	57.8 (52.6-63.8)	51.3 (47.9-55.3)	32.3 (30.9-33.8)	30.8 (29.0-32.1)	39.9 (34.6-44.2)	63.6 (57.1-69.0)
♀ (N=19)	76.8 (70.2-98.7)	54.5 (49.0-56.3)	34.8 (31.8-36.4)	33.7 (31.8-35.8)	44.5 (41.5-48.4)	63.6 (66.7-83.1)
Osteopilus septentrionalis						
♂ (N=40)	55.3	°45.8	°33.4 (31.9-34.8)	31.8	°30.8 (30.4-31.2)	°66.4 (62.8-70.0)
♀ (N=17)	75.2	°46.9	°35.2 (34.5-35.9)	33.3	°39.7 (31.4-45.0)	°77.1 (75.8-78.4)
Hyla vasta						
♂ (N=12)	96.7 (87.5-108.8)	53.4 (49.3-56.4)	31.7 (30.3-34.1)	33.4 (31.7-35.3)	26.2 (24.8-27.8)	58.4 (51.0-71.0)
♀ (N=2)	136.9 (131.8-141.9)	51.0 (49.8-52.2)	30.0 (29.5-30.4)	32.2 (31.8-32.6)	34.1 (33.9-34.2)	57.8 (57.6-58.0)
Calyptahyla lichenata						
♂ (N=1)	92.6	-----	35.4	39.0	35.1	68.2
♀ (N=1)	104.0	53.9	38.4	41.8	34.5	84.8

peninsular Florida and Puerto Rico. Cuba differs from the smaller islands of Hispaniola and Jamaica in lacking a central highland mass; its mountainous areas are disjunct. A relatively low chain occurs on the western end of the island with peaks reaching elevations of 728 m. South-centrally, the peaks of a small mountain mass reach 1156 m. The most extensive montane area lies along the southeastern coast and on the eastern end of the island where peaks reach elevations above 2000 m. There are restricted areas of mixed pine and broadleaf forests in the extreme eastern and western montane areas. Two low, isolated highland masses (*ca.* 310 m elevation) occur on the Isle of Pines. Tropical rainforest occurs principally in the south-central montane area of Cuba, whereas the southeastern coast supports xeric-adapted vegetation. Save for coastal mangrove and xeric scrub areas, most of Cuba is characterized by park-savanna vegetation of scattered palms and scrub. *Hyla septentrionalis* is widespread on Cuba and the Isle of Pines at low to moderate elevations, where it inhabits old cisterns, axils of palm leaves, banana plants, and drain pipes; eggs are laid in temporary drainage ditches, flooded basements, and old cisterns (Carr, 1940). Little is known concerning its habits in natural situations.

The Bahamas.—The Bahama archipelago consists of some 29 major islands extending about 1128 km northwest to southeast. The relief of the islands is below about 67 m. Some of the larger islands are characterized by lengthwise ranges of hills, whereas others (*e.g.*, the large island, Andros) have virtually no topographical relief. Running streams are rare and availability of fresh water is seasonal, depending upon rainfall. Vegetationally, the islands are characterized by coppice thorn bush and dry scrub. *Hyla septentrionalis* is the only treefrog occurring naturally in the Bahamas; it has been reported from the Cayman Islands in addition to Little Bahama Bank, Grand Bahama Bank, San Salvador, Rum, Crooked and Acklin's Islands. The species was introduced recently to Great Inagua Island (Schwartz, 1968). *Hyla septentrionalis* has become well established in southern peninsular Florida, where it occurs sympatrically with several North American hylids (Duellman and Schwartz, 1958).

Puerto Rico.—The island of Puerto Rico has no native treefrogs. *Hyla septentrionalis* and *H. cinerea* are recent adventives (Duellman and Crombie, 1970; Schwartz, pers. com.). The island, although small (*ca.* 160 x 48 km), is topographically diverse. The elevation of the central highlands reaches approximately 1220 m. A relatively narrow area of savanna-parkland occurs along the margin of Puerto Rico. Mixed pine and broadleaf forests predominate in the central hills and tropical rainforest is restricted to the higher, central elevations.

ANALYSIS OF CHARACTERS

External morphology.—Tables 1 and 2 summarize data on the sizes and proportions of nine species of the West Indian hylid fauna. Although the quality of these data vary with respect to sample size and uniformity, they are sufficient to substantiate several observations on the physical features of these frogs. The species (*wilderi, marianae, pulchrilineata,* and *heliprini*) included in table 1 are small to moderate-sized frogs which range in mean size from 27.3 to 49.4 mm snout-vent length. The species (*brunneus, dominicensis, septentrionalis, vasta,* and *lichenata*) listed in table 2 are moderate to large frogs with snout-vent lengths between 60.5 to 136.9 mm. Ratios of tibia to snout-vent length are remarkably uniform among all species, with values lying between 46.9 and 54.5 percent; similarly the ratios of head length and width to snout-vent length vary little (30.0-39.0%). In contrast to the proportional uniformity of the foregoing measurements, the ratio of interorbital distance to head width parallels the pattern evident in overall size of frogs. The smaller species included in table 1 have relatively narrower interorbital areas (28.1-33.8%) than do the larger species (*brunnea, dominicensis, septentrionalis, vasta,* and *lichenata*) of table 2 (30.8-44.5%). Likewise, relative to the diameters of the eyes, the tympana of the smaller species are smaller (50.4-61.1%) than those of the larger species (57.8-77.1%). Among the group of larger frogs, the tympanum-eye ratio of *Hyla vasta* is noticeably lower (*ca.* 58%) than the other species (63.6-77.1%). Visual inspection shows the tympanum of *vasta* to be small; the eye is not distinctly large.

The dorsal skin of *wilderi, pulchrilineata, marianae,* and *heilprini* is smooth. That of *dominicensis* and *brunnea* is smooth; however the latter has scattered, small, round tubercles on the forearm. *Hyla septentrionalis* and *vasta* have similar tubercles scattered over the entire dorsum. In contrast to the other species, the dorsum of *lichenata* is strongly tubercular. The ventral skin of all species is granular to some degree. It is weakly granular on the abdomen and thighs of all the smaller species, except *heilprini,* in which it is coarsely granular; *wilderi* and *marianae* are distinguished by the presence of tubercles around the cloaca and *heilprini* by the presence of a large, dermal submental gland. Granulation is moderately developed on the posterior abdomen and around the cloaca in *brunnea.* In *septentrionalis* it extends over the thighs and entire abdominal area, but is absent around the cloaca. The ventral regions of *dominicensis, lichenata,* and *vasta* are both coarsely granular; *lichenata* is further distinguished by tubercular skin around the cloaca.

Fringes are absent from the limbs of all species except *vasta* and *lichenata.* In the latter, a distinct dermal fringe is present along the outer edge of the forearm and tarsus. *Hyla vasta* bears more ex-

tensive fringes along the forearm and the hind limb, extending the length of the tarsus and foot. In addition, it has a distinct series of tubercles on the mandible and a proliferation of tubercles at the tibia-tarsal joint. Dermal wrist folds are absent in all of the smaller species except *septentrionalis.*

The tympanum is distinct in each species except *wilderi,* in which it is not obvious externally, and *heilprini,* in which it is "concealed." Similarly, the supratympanic folds are scarcely evident in these two species, whereas they are distinct in the others. The nostrils are terminal in all species, but vary in their degree of protuberance. In most the nostrils are not protuberant. They are slightly protuberant in *dominicensis, lichenata,* and *brunnea,* and noticeably protuberant in *vasta.* The cloacal opening lies posteriorly at the upper level of the thighs in all species. Dermal modifications in the cloacal region are absent in all species, except *lichenata, vasta,* and *heilprini.* A small horizontal supracloacal flap characterizes *lichenata,* whereas longitudinal folds of skin lie adjacent to the cloaca in *heilprini.* A profusion of tubercular skin growths distinguish *vasta.*

Hands and feet.—Hand morphology varies considerably among the West Indian hylids. All species have well-developed digital pads which are larger on the fingers than on the toes. *Hyla heilprini* is unique in having a prepollex which is evident externally, and a well-developed prepollical spine. Webbing is absent from the hand in *wilderi* and present basally between the fingers in *marianae, pulchrilineata,* and *septentrionalis.* Of the remaining species, the fingers of *brunnea, dominicensis* and *lichenata* are approximately one-fourth webbed, whereas those of *heilprini* are one-half webbed and those of *vasta* three-fourths webbed. Subarticular tubercles are distinct and round on inner digits with a tendency toward becoming flattened and bifid on outer fingers in all species except *wilderi,* in which all subarticular tubercles are low, round, and barely evident. Supernumerary tubercles vary from total absence in *marianae* and *pulchrilineata,* to presence of a few indistinct tubercles in *vasta* and *wilderi,* a moderate number of low, round tubercles in *lichenata* and *septentrionalis,* and presence of numerous tiny tubercles in *brunnea, dominicensis,* and *heilprini.* All species have inner palmer tubercles which are more or less elliptical in shape. Distinct outer palmar tubercles are absent in five species; whereas in the remaining four (*wilderi, dominicensis, vasta,* and *pulchrilineata*) two outer palmar tubercles are present. Males of at least seven of the species bear nuptial excrescences; these vary from flat horny pads in *marianae, pulchrilineata, dominicensis, septentrionalis* and *vasta,* to a proliferation of small, keratinous granules in *brunnea,* and the presence of large keratinous spines in
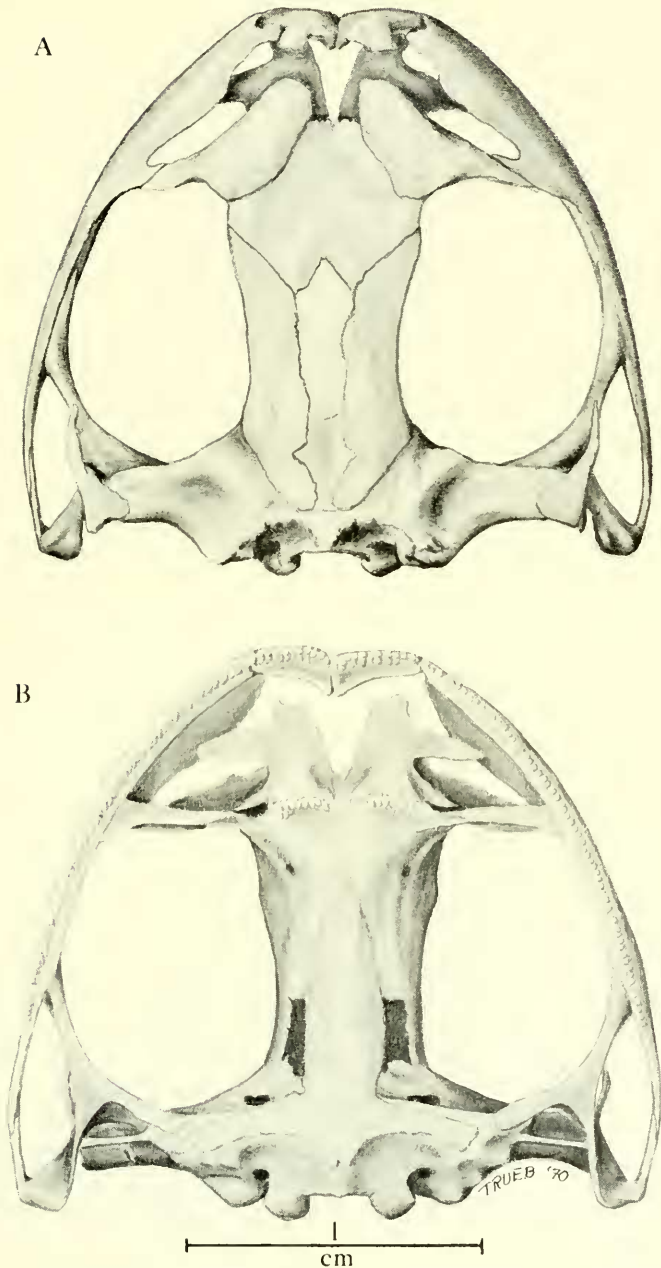
FIG. 4. Skull of *Hyla vasta* (University of Kansas, Museum of Natural History 84711). A. Dorsal view. B. Ventral view.

wilderi. Nuptial excrescences are absent in *heilprini;* their presence or absence has not been noted in *lichenata.*

Webbing is present between the toes and more extensively developed in all species than finger webbing. The toes of *wilderi* are about one-fourth webbed, those of *marianae* one-third and *pulchrilineata* and *septentrionalis* two-thirds webbed. The feet of *brunnea, dominicensis,* and *lichenata* are three-fourths webbed, whereas those of *vasta* and *heilprini* are fully webbed. Subarticular tubercles are round; they have a tendency to be flattened and bifid on the outer toes of *dominicensis, heilprini,* and *lichenata.* Plantar supernumerary tubercles are absent in *vasta* and *heilprini,* and few in number in all other species except *brunnea* and *lichenata,* in which their numbers are moderate. Inner metatarsal tubercles are present and vary between ovoid and flat, and elliptical and elevated in shape. Outer metatarsal tubercles are absent or scarcely evident in all species except *pulchrilineata, marianae* and *lichenata;* the tubercles are small and round in the latter species.

Cranial Osteology.—On the basis of cranial characteristics, the West Indian hylid fauna is easily subdivided into the small-sized and large-sized groups observed in tables 1 and 2. Although the observed classes correlate with body size, they are predicated on structural features of the skulls and will be discussed separately. Among the larger species there are three groups. The first is composed of *septentrionalis, dominicensis,* and *brunnea,* whereas the second and third groups each contain only one species, *lichenata* and *vasta,* respectively.

Despite being the largest of the West Indian frogs (Table 2), *vasta* has the least well ossified skull (Fig. 4); it is only slightly wider than long and has no dermal modifications. The skulls of the moderate-sized *septentrionalis*-group also are slightly wider than long but, are distinguished by exostosis, casquing, and co-ossification (Fig. 5). A moderate development of dermal sculpturing resulting in patterns of pits, ridges, and bony tubercles is associated with this group. *Hyla lichenata* is distinctively different from both *vasta* and the *septentrionalis* group. The skull (Fig. 6) is distinctly wider than long and heavily exostosed, casqued, and co-ossified. Dermal sculpturing consists of a distinctive pattern of peripheral, radial ridges which grade into a central pattern of pits and ridges.

The skull of *vasta* is minimally roofed and delicate in structure (Fig. 4A). A dermal sphenethmoid is absent. Although nasals are moderately large, they are widely separated and barely overlap the anterior margin of the sphenethmoid. Similarly, the frontoparietals are minimally developed. They are not peripherally expanded and do not articulate with the maxillary. The palatines (Fig. 4B) are well developed, anteriorly convex, and articulate with the lateral edge of the sphenethmoid. The parasphenoid is large. The cultri-
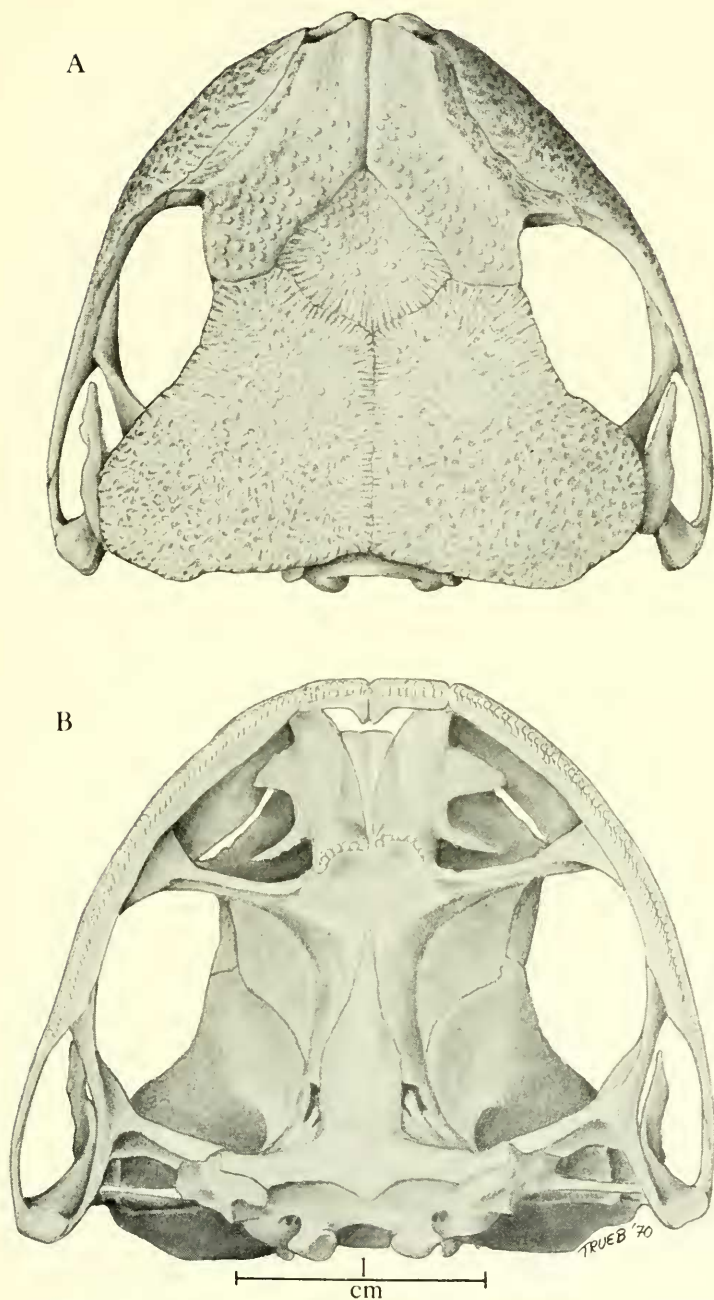
Fig. 5. Skull of *Osteopilus brunneus* (University of Kansas, Museum of Natural History 84693). A. Dorsal view. B. Ventral view.

form process of this element is edentate and extends to the forepart of the orbit. The alae are posterolaterally inclined; their distal ends are widely separated from the medial rami of the pterygoid bones. The pterygoids are robust, triradiate and fully articulated; the anterior rami articulate with the maxillaries at the mid-level of the orbits. The prevomers are widely separated from the maxillary arch. Prevomerine teeth are situated on moderately broad, curved elevations and occur in a double row laterally.

Cranially, *dominicensis, septentrionalis* and *brunnea* represent a group of broadly casqued, moderately exostosed, co-ossified hylids. Each species is characterized by a pattern of dermal sculpturing which consists of irregularly shaped pits and ridges, and proliferations of small, bony tubercles (Fig. 5A). Along the margins of the dermal roofing bones and the maxillae, the tubercles tend to be aligned in series to produce patterns of low radial ridges. A dermal sphenethmoid is present in each species. The frontoparietals are extensively developed; a broad supraorbital flange is present and the paired elements articulate medially, completely obscuring the frontoparietal fontanelle. Posterolaterally, the frontoparietal completely roofs the prootic region in mature females of each species. In *septentrionalis* and *dominicensis* the frontoparietal articulates with the otic arch of the squamosal, whereas no articulation is established between these elements in *brunnea*. The occipital margins of the frontoparietals are strongly convex in *dominicensis* and *brunnea*, but tend to be straight in *septentrionalis*. The nasals are extensive and with all adjacent elements articulated in all three species. The canthal ridges are straight in *dominicensis*, very slightly concave in *septentrionalis*, and markedly concave in *brunnea*. Furthermore, *brunnea* has a much longer medial nasal articulation than the other two species. In *dominicensis* and *septentrionalis*, the zygomatic arch of the squamosal articulates with the maxillary, whereas the arch is incomplete in *brunnea*. Palatines are well developed in *brunnea* and *septentrionalis*, but very poorly developed in *dominicensis*. In contrast to the condition of *vasta*, the palatines of the *septentrionalis* group tend to be straight or to have their proximal ends turned anteriorly (Fig. 5B). The cultriform process of the parasphenoid is edentate and extends to the anterior level of the orbit in each species. The parasphenoid alae are perpendicularly oriented in *dominicensis* and *brunnea* and slightly inclined posterolaterally in *septentrionalis*. Likewise, the distal ends of the alae are narrowly separated from the medial pterygoid ramus in *dominicensis* and *brunnea* and widely separated in *septentrionalis*. The pterygoid is best developed in *brunnea*, in which the anterior arm articulates with the maxillary at the mid-level of the orbit and the medial arm articulates firmly with the otic capsule. The element is less robust and articulates with the maxillary at the
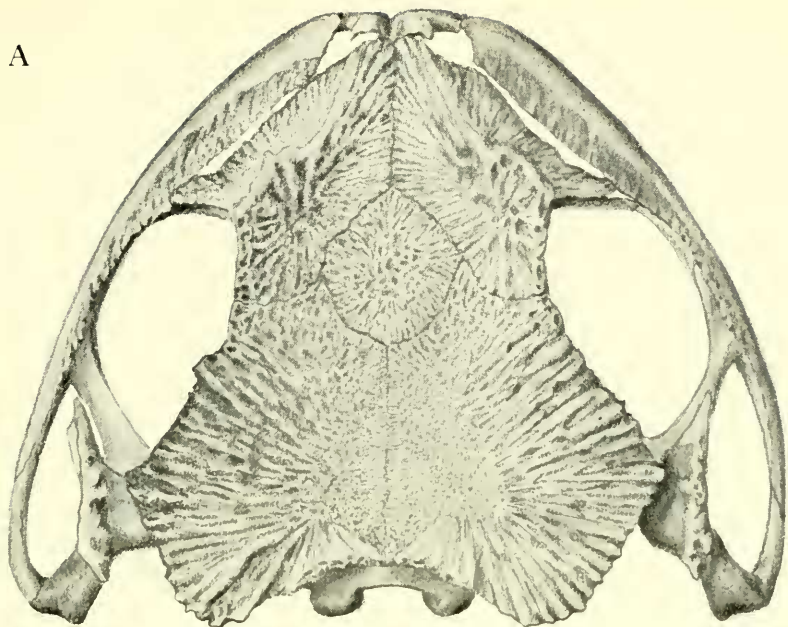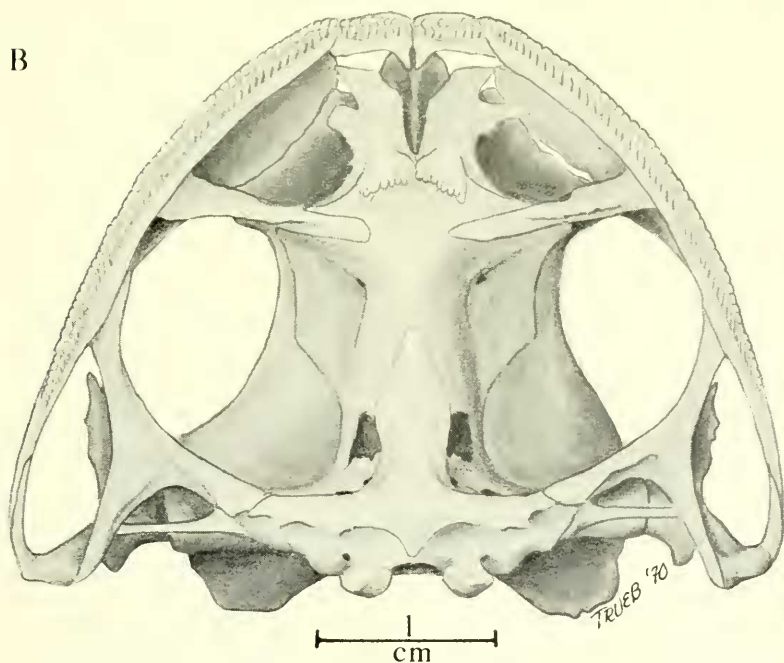
FIG. 6. Skull of *Calyptahyla lichenata* (British Museum of Natural History 52.12.1). A. Dorsal view. B. Ventral view.

posterior level of the orbit in *dominicensis* and *septentrionalis*. In the latter species the medial pterygoid ramus is weakly articulated with the otic capsule, whereas in *dominicensis* the articulation is absent. The prevomers of the three species are similar in having single rows of teeth situated on broad, curved elevations. The prevomers are small and widely separated from the maxillary arch in *dominicensis*, whereas they are large and articulate with the maxillary arch in *septentrionalis* and *brunnea*. *Hyla brunnea* is further distinguished by the strong curvature of the prevomerine tooth row (Fig. 5B).

The skull of *lichenata* is distinctly different from those of the other four species. Like the *septentrionalis*-group, it bears a dermal sphenethmoid and is broadly casqued and co-ossified. However, the skull is considerably broader than long and the pattern of exostosis (Fig. 6A) consists of rugose peripheral ridges which grade into a central pattern of bony pits and ridges. Although the skull is heavily casqued, it is less well developed than in the *septentrionalis* group. The nasals are not completely articulated with the maxillaries. The frontoparietals extend posterolaterally over the otic region but are widely separated from the squamosal. The zygomatic arch of the squamosal does not articulate with the maxillary. The palatines are robust and straight (Fig. 6B). The cultriform process of the parasphenoid is edentate and exceptionally short, extending only to the mid-level of the orbit. The parasphenoid alae are oriented perpendicularly and articulate distally with the medial rami of the pterygoids. The pterygoids are extremely robust and fully articulated; the medial ramus articulates with the maxillary at the mid-level of the orbit. The prevomers are moderate-sized bones separated from the maxillary arch. They bear single rows of teeth on elevations which are only slightly curved and oriented at a slight angle to one another.

The cranial characteristics of the smaller members of the Western Indian hylid fauna (*wilderi, marianae, heilprini*, and *pulchrilineata*) clearly represent the cumulative effect of different kinds of adaptive trends than those evident among the larger frogs. Correlated with their smaller body sizes (*ca.* 25-50 mm), the dimensions of the skulls are decreased, and ossification is reduced. The latter is especially evident in the absence of dermal modifications (including the absence of the dermal sphenethmoid), and the moderate to minimal development of dermal roofing bones; the frontoparietal foramen is evident in each species. The mandibles are incompletely articulated and, similarly, suspensory and bracing elements (squamosal, palatine, and pterygoid) tend to be reduced in size and incompletely articulated. Three different patterns of cranial architecture are evident among these smaller hylids. The skulls of *marianae* (Fig. 8) and *wilderi* (Fig. 9) are characterized by the most
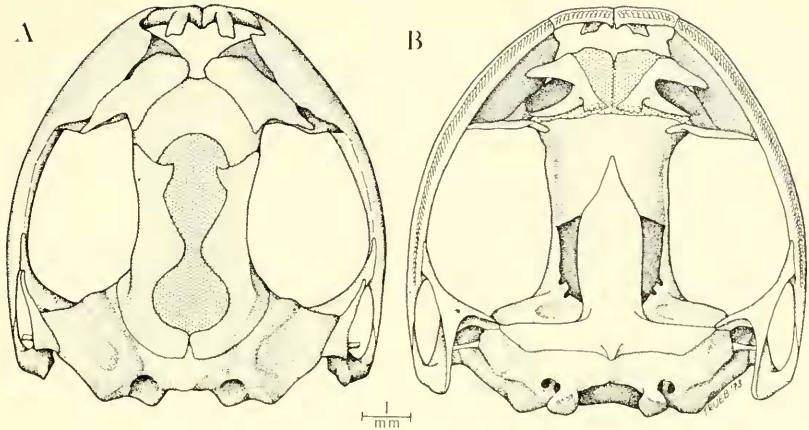
FIG. 7. Skull of *Hyla pulchrilineata* (University of Kansas, Museum of Natural History 84709). A. Dorsal view. B. Ventral view.

marked reduction in ossification and by snouts which (in dorsal view) are broadly rounded. The skull of *pulchrilineata* (Fig. 7) is easily distinguished by its length and narrowness, and that of *heilprini* (Fig. 10) by its truncate snout.

The narrow skull of *pulchrilineata* (Fig. 7A) is the most distinctive of these four species. The nasals are approximately rectangular in dorsal view and about twice as long as wide; their longitudinal axes nearly parallel those of the maxillary arch. About one-third of the length of the nasal projects anterior to the sphenethmoid. The premaxillary bears long, dorsolaterally divergent alary processes, but only a reduced palatine projection vetromedially. The prootic is narrow and laterally, abuts (but is not overlapped by) the otic ramus of the squamosal. The zygomatic ramus of this element extends approximately one-third the distance to the maxillary. The palatines are reduced, non-articulate and anteriorly concave (Fig. 7B). The parasphenoid bears a large cultriform process; the anterior end of the process is truncate and lies at the forelevel of the orbit. The pterygoid is small; the anterior ramus articulates with the maxillary at the posterior level of the orbit, whereas the medial arm does not bear a bony articulation with the otic capsule. The prevomers are small but bear moderately large dentigerous processes. These processes are curved (anteriorly concave), and narrowly separated; each bears a single row of approximately nine teeth.

The relatively greater breadth of the skulls of *wilderi* and *marianae* (Figs. 8 and 9) readily distinguishes them from *pulchrilineata*. The nasals are only slightly longer than wide, and their longitudinal axes parallel the maxillary arch. One-third (*wilderi*) to one-half
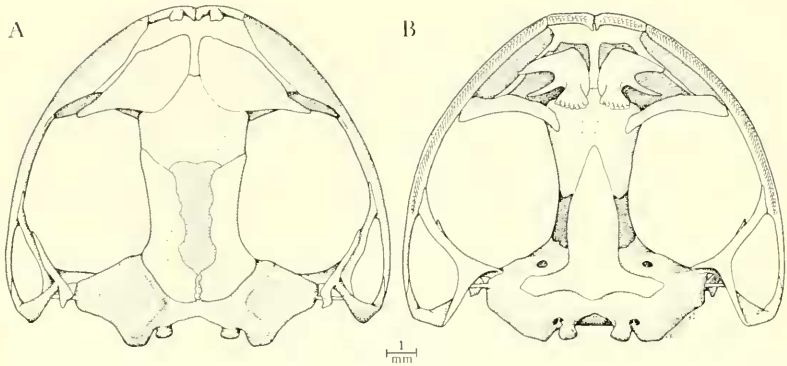
FIG. 8. Skull of *Hyla marianae* (University of Kansas, Museum of Natural History 146838, female). A. Dorsal view. B. Ventral view.

(*marianae*) the length of the nasal lies anterior to the sphenethmoid. The nasals of both species differ from those of *pulchrilineata* in having convex medial margins which broadly overlap the sphenethmoid. The alary processes of the premaxillary are moderately long in *marianae* as contrasted with *wilderi*; the processes are nearly vertical in both species. The palatine projection of the premaxillary is small in *wilderi* and minute in *marianae*. Like *pulchrilineata*, both *marianae* (Fig. 8A) and *wilderi* (Fig. 9A) have reduced prootics; but unlike the former, the otic rami of the squamosals in *marianae* and *wilderi* do not articulate with the prootics. Moreover, the zygomatic rami of the squamosals are longer, extending about one-half the distance to the maxillaries. The palatines of *wilderi* and *marianae* are anteriorly convex in contrast to those of *pulchrilineata*. Those of *wilderi* (Fig. 9B) are reduced; they articulate with neither the maxillary nor the sphenethmoid, whereas the palatines of *marianae* (Fig. 8B) extend from the maxillary to articulate firmly with the sphenethmoid. The parasphenoids of both species are similar. The cultriform process of this element is edentate, acuminate anteriorly, and terminates at a level in the anterior third of the length of the orbit. The parasphenoid alae are widely separated from the medial rami of the pterygoid. The pterygoid of *marianae* is moderate in size and fully articulated; in contrast, that of *wilderi* is small and lacks a medial articulation with the otic capsule. The anterior rami of the pterygoids of both species articulate with the maxillaries at the posterior levels of the orbits. The prevomers of *marianae* are relatively larger than those of *wilderi*. The bones are widely separated from the maxillary arches in both species and bear similar dentigerous processes which are straight, widely separated elevations. The processes bear single rows of teeth totaling 7-8 per row in *marianae* and 4-5 per row in *wilderi*.
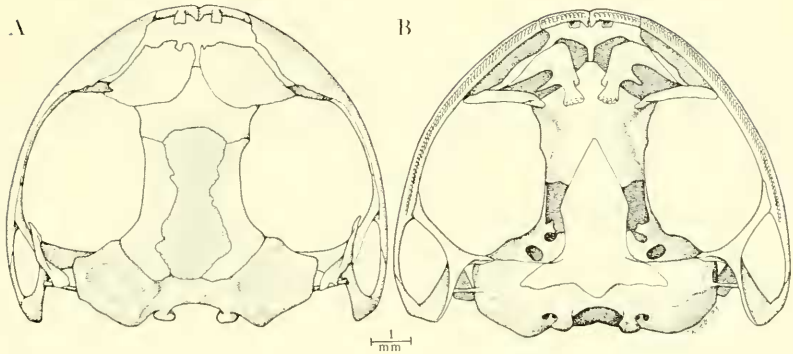
FIG. 9. Skull of *Hyla wilderi* (University of Kansas, Museum of Natural History 84713, female). A. Dorsal view. B. Ventral view.

Several features set apart the skull of *heilprini* (Fig. 10). Most apparent is its blunt, truncate snout. Unlike the other three species, the nasals are long and narrow (at least three times as long as the greatest width). Furthermore, the nasals are acuminate anteriorly with their anterior ends converging at the margin of the sphenethmoid. The longitudinal axes of the nasals are not parallel to the maxillary arch. The frontoparietals of *heilprini* are poorly developed; thus a large part of the frontoparietal fontanelle is evident, particularly posteriorly. The premaxillary differs in several respects from those of the other small hylids. The alary processes are moderately small, dorsomedially convergent, and posteriorly inclined; the palatine processes are well developed. The prootics are wide in contrast to those of *pulchrilineata, marianae,* and *wilderi.* The squamosals overlap the prootics dorsolaterally and the zygomatic rami extend approximately one-half the distance to the maxillaries. The palatines are delicate, anteriorly convex, and articulate with the sphenethmoid medially. The parasphenoid is similar in structure to those of *marianae* and *wilderi,* differing from the latter and *pulchrilineata* in having alae which are only narrowly separated from the medial rami of the pterygoids. The pterygoids of *heilprini* are moderately large and fully articulated. The anterior pterygoid rami are much longer than those of the other species; they articulate with the maxillaries at approximately the midlevel of the orbit. The prevomers are moderately large and not closely associated with the maxillary arch. Each element bears a single row of teeth (5-6 per row) on a slightly curved elevation.

Axial osteology.—The vertebral columns of the West Indian hylids are uniformly characterized by eight procoelous, presacral vertebrae, none of which is fused. The cervical cotyles are widely separated, and there are no dermal modifications. The sacral vertebrae bear bicondylar articulations with unmodified coccyges. Within
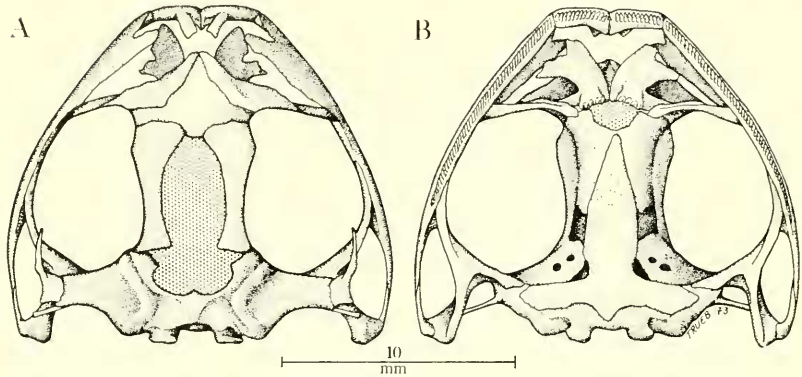
FIG. 10. Skull of *Hyla heilprini* (University of Kansas, Museum of Natural History 90838, male). A. Dorsal view. B. Ventral view.

these generalized limitations, there are morphological patterns (Fig. 2 A and B) which corroborate the species groups established on the basis of cranial structure. The presence of neural spines on the presacral vertebrae of the larger species distinguishes them from the smaller frogs.

Among the larger members of the West Indian frogs, *lichenata* and *vasta* show the most specializations in the vertebral column associated with a trend towards advanced terrestrialism (*i.e.*, arboreality); in general, these modifications are most pronounced in *lichenata*. Although the neural spines are best developed on presacrals I-V, they are present on all presacrals of *lichenata*. In *vasta*, the neural spines are obvious on presacrals I-IV and barely visible on the remaining presacrals. In both of these species (in contrast to the other frogs) the sacral diapophyses are wider than the widest transverse processes (presacral III); the diapophyses are proportionately widest in *lichenata*. The transverse processes are of nearly uniform width in *lichenata;* presacral III comprises 87 percent of the width of the sacral diapophyses, and each of presacrals IV-VIII, 75 percent of the sacral width. The pattern is less uniform in *vasta* (III—95% of the sacral width, IV—81%, and V-VIII—71%). In both species the transverse processes of presacral II and III are expanded distally. *Hyla lichenata* differs from *vasta* in bearing a small flange on the anterior margin of the transverse process of presacral II and a similar flange on the posterior margin of the transverse process of presacral III. The sacral diapophyses are only slightly dilated in *vasta* (*ca.* 20° and *lichenata* (*ca.* 31°). The differential expansion is the result of the orientation of the anterior margin of the sacral diapophyses. The orientation may be measured by calculating the angle between the anterior edge of the sacral diapophysis and the

longitudinal axis of the body. The angle approximates 80° in *lichenata* and 103° in *vasta*.

The vertebral columns of the *septentrionalis*-group (*septentrionalis, dominicensis,* and *brunnea*) show fewer advanced terrestrial specializations than those of *vasta* and *lichenata* (Fig. 2). Neural spines are best developed in *dominicensis,* in which they are evident on presacrals I-V; in *brunnea,* spines are present on presacrals I-IV, whereas in *septentrionalis* they are invariably present only on presacrals I-III. The sacral diapophyses of all three species are narrower than the widest transverse process of the presacrals (III), in contrast to *vasta* and *lichenata*. The transverse processes of the presacrals tend to be subequal in width. In *brunnea,* presacral III comprises 109 percent of the width of the sacral diapophyses, IV—89 percent, each of V and VI—79 percent, VII—75 percent, and VIII—72 percent. The pattern is nearly the same in *dominicensis* except that presacral VIII is slightly wider than VII. *Hyla septentrionalis* demonstrates the strongest tendencies towards terrestrial modifications of the axial skeleton in this group; the transverse processes are more nearly equal in width (III—113% of sacral width, IV—100%, V—93% VI—87%, VII and VIII—85%). All three species are characterized by distal expansion of the transverse processes of presacral II and III. A minute anterior flange is present on the transverse process of presacral II in *brunnea;* a similar, but much larger flange is present in *septentrionalis.* The sacral diapophyses are more broadly dilated in all three species than in *vasta* or *lichenata.* The angle of expansion is about 41° in both *brunnea* and *dominicensis,* and approximately 57° in *septentrionalis.* The corresponding anterior sacral angles are 70°, 74°, and 82° in *septentrionalis, dominicensis,* and *brunnea,* respectively.

The vertebral columns of the smaller hylids tend to show fewer specializations and greater uniformity of pattern than those of the larger frogs. In each of the four species, neural spines are absent and the width of the transverse processes of presacral III is greater than the width of the sacral diapophyses. The transverse processes lack flanges, and the sacral diapophyses are moderately dilated (43-48°). In *pulchrilineata,* which probably has the most generalized axial structure of the groups, the width of presacral III comprises 117 percent of the width of the sacral diapophyses. The widths of the transverse processes of the presacrals are subequal except those of VII and VIII (III—117%, IV—98%, V—85%, VI—80%, and VII and VIII—73%). The transverse processes of presacrals II, III, and IV are slightly expanded distally. The angle between the anterior edge of the sacral diapophysis and the longitudinal axis of the body is 77°; the corresponding posterior angle is 55°.

In the remaining three species (*heilprini, wilderi,* and *marianae*), only the transverse processes of presacral III are expanded distally.

Of the three, the axial morphology of *heilprini* is most similar to *pulchrilineata,* although the two are readily distinguishable. The presacrals of *heilprini* are clearly subequal in width (III—111% of sacral width, IV—96%, V—87%, VI—86%, VII—80%, and VIII—75%). The sacral diapophysis expansion is nearly the same as *pulchrilineata* (anterior angle, 77°; angle of expansion, 45°). Of the smaller species, *marianae* and *wilderi* show the highest degree of axial specialization. The relative widths of the transverse processes are slightly subequal in *marianae* (III—110% of sacral width, IV—97%, V—86%, VI—84%, VII—83%, and VIII—79%) and more nearly uniform in *wilderi* (III—105% of sacral width, IV—90%, and V-VIII —80%). The orientation and expansion of the sacral diapophyses is similar in both species. The anterior sacral angles are 75° and 80° in *marianae* and *wilderi,* respectively. Corresponding angles of sacral expansion are 43° and 48°.

Pelvic osteology.—In general, the pelvic structure of the West Indian hylids is quite generalized (Fig. 2C). The ilium and ischium are ossified and the pubis is cartilaginous or secondarily calcified in larger species. Dorsal acetabular expansion is minimal. Ilial protuberances are present, but moderately developed in all species. The ilium is devoid of dorsal crest and lateral expansions in all species except *marianae* in which a low crest is present.

Values for relative ilial length (measured as a function of the length of the acetabular portion of the girdle) are *pulchrilineata,* 3.8; *dominicensis,* 3.7; *septentrionalis* and *brunnea,* 3.6; *vasta,* 3.5; *lichenata,* 3.3; *wilderi,* 2.9; and *marianae,* 2.1. One pattern emerges which apparently is independent of body size. Among the smaller frogs, the species with the least specialized vertebral column structure (*pulchrilineata*) has the longest ilium. Similarly, the more generalized of the larger species (*septentrionalis* group) tend to have longer ilia than the more specialized *vasta* and *lichenata.* The *septentrionalis* group is characterized by obtuse angles between the ilial shaft and the preacetabular margin; that of *vasta* approaches 90°, whereas the angle is acute in *lichenata. Hyla heilprini* has an obtuse preacetabular angle; the angles of *pulchrilineata* and *wilderi* approximately 90° and that of *marianae* is acute.

Throat musculature and vocal sac structure.—All members of the West Indian hylid fauna have vocal sacs except *marianae.* The larger frogs are uniformly characterized by: 1) a posterolateral attachment of the fibers of the intermandibularis upon the ventral surface of the submentalis; 2) vocal sacs which are confined to a position above the interhyoideus muscle; and 3) presence of the adductor mandibulae externus superficialis. The *septentrionalis*-group is distinguished from *vasta* and *lichenata* by the differentiation of the intermandibularis to form a supplementary, apical element (Fig. 11). Most hylids, like *vasta* and *lichenata,* have an
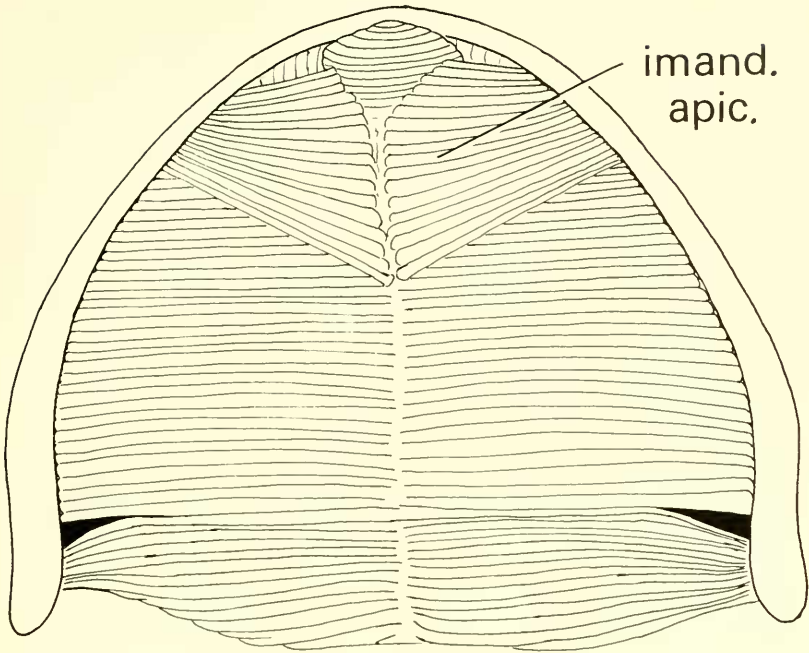
imand. apic.

FIG. 11. Superficial mandibular musculature of *Osteopilus brunneus*. Abbreviations: *imand. apic.*, supplementary apical element of *M. intermandibularis*.

undifferentiated intermandibularis (Tyler, 1971). The interhyoideus muscle shows some variation in the development of lateral lobes. The lobes are absent in *brunnea* and *lichenata;* they are present and located posterior to the mandible in *dominicensis* and *vasta.* In *septentrionalis,* the lobes are present, small in size, and situated above the mandible. Similarly, the nature of the medial attachment of the intermandibularis muscle varies. In *dominicensis* and *septentrionalis,* the muscles meet at a tendinous raphe, whereas a slender aponeurosis is present in *lichenata* and *brunnea,* and a broad aponeurosis in *vasta.*

In *brunnea* the vocal sac apertures are present as slits of moderate length, each being equivalent to approximately one-third of the length of the mandible. The remaining large species are characterized by vocal sac apertures which are small, circular orifices equivalent to one-eighth to one-tenth of the length of the mandible. This condition occurs infrequently in hylid frogs and represents a specialization over the moderate-sized slit.

There are only two features common to all of the smaller species: (1) Absence of differentiation of the intermandibularis; (2) absence of the *adductor mandibulae externus superficialis.* Postero-

lateral attachment of the fibers of the intermandibularis upon the ventral surface of the submentalis occurs in *marianae, pulchrilineata,* and *wilderi* but not *heilprini,* where *pulchrilineata* is the only species lacking a median aponeurosis of the intermandibularis. The interhyoideus is least developed in *marianae,* which is unique in lacking a vocal sac, and most highly developed in *pulchrilineata,* in which there is a distinct, posterior, bilobular, supramandibular orientation.   The remaining species have developed unilobular, postmandibular vocal sacs. In all species the vocal sac apertures are slit-like and approximately one-third of the length of the mandibles.

Hyla heilprini is unique in possessing a dermal, submental gland comparable to that occurring in *H. colymba,* which is illustrated by Duellman (1970).

Extrinsic musculature of the cloaca.—The cloaca of all West Indian hylids is characterized by the presence of the protractor cloacae (Fig. 3). The muscle constitutes a bilateral extension of the ventral lip of the cloacal orifice, functionally permitting protraction of the orifice. The muscle occurs in all North American hylids examined, all casque-headed hylids, is present or absent in *Hyla* from Middle and South America, and does not occur in any from Australia and New Guinea.

The only observed variation among the West Indian species is the inferior boundary of the protractor cloacae, and the nature of its attachments to the ischial ridge. In the larger species either a few muscle fibers or the median tendon extend to the ventral surface of the ischial ridge (Fig. 3). In the smaller species the muscle always terminates at the position posterior to the gracilis minor where the lateral halves of the protractor cloacae unite. From that site a very short tendon attaches to the posterior face of the ischial ridge.

Breeding sites and larval morphology.—The four Jamaican species (*brunnea, lichenata, wilderi,* and *marianae*) are known to breed only in bromeliads. None of the remaining species has been observed to utilize bromeliads for breeding. *Hyla septentrionalis* is apparently restricted to ponds and cisterns, whereas *vasta* and *dominicensis* utilize streams as well as pools. *Hyla heilprini* breeds in torrential streams. No observations are recorded in the literature on either the breeding site or the larvae of *pulchrilineata.*

The tadpoles of these frogs are diverse morphologically and easily distinguishable. The most generalized larvae are associated with the pond breeders. Noble (1927) reported that *dominicensis* laid its eggs in stagnant pools of rainwater in the forest or along the edge of a stream bank. The larva of *dominicensis* is characterized by a short tail with well-developed fins, an interrupted labial disc and a 2/5 tooth row pattern. The tadpole of *septentrionalis*

is similar, save for a 2/4 tooth row pattern. *Hyla vasta* lays its eggs in basins in gravel and stones on the edges of stream pools (Noble, 1927); subsequent to hatching, the larvae move from the basins over wet stones into the stream. The larvae of *vasta* have a short, thick, muscular tail with deep fins, an uninterrupted labial disc, and minimally, a 4/6 tooth row pattern. The larvae of *heilprini* are the most obviously stream adapted with extremely thick, muscular tails, deep fins, uninterrupted labial disc and a 6/9 tooth row pattern. Relative to the non-bromeliad tapoles, the bromeliad larvae have longer tails, reduced fins, and reduced numbers of toothrows. The larvae of both *brunnea* and *lichenata* have incomplete labial discs and a tooth row pattern of 1/0; the tail of the *lichenata* larva is somewhat shorter than that of *brunnea*. The labial discs are complete in the larvae of *marianae* and *wilderi;* furthermore, tooth rows are absent and the lower beaks are unnotched in contrast to the remaining species. The tadpole of *wilderi* can be distinguished from that of *marianae* by the relatively shorter tail and presence of keratinous structures around the margin of the labial disc in the former.

RELATIONSHIPS OF THE WEST INDIAN HYLIDS

Our previous understanding of the West Indian hylids has been based principally on the work of Dunn (1926) and subsequent commentary by Noble (1927, 1931) and Williams *et. al.* (1963) who focused attention on the apparently complex and peculiar relationships of these frogs. Careful perusal of Dunn's (1926) discussion of the West Indian hylids yields several interesting observations. Dunn considered *brunnea, septentrionalis,* and *dominicensis* to be closely related; he was the first to recognize them as the *septentrionalis* group. Similarly, he implied a relatively close relationship between *wilderi* and *marianae.* Dunn obviously was perplexed by the distributional symmetry of the small and large species (*i.e.,* the occurrence of two large species in combination with two smaller species on both Jamaica and Hispaniola), in contrast to the insular divergence of breeding habits (*i.e.,* bromeliad breeders on Jamaica as opposed to the more generalized pond and stream breeders of Hispaniola). It is implicit, although not directly stated in his discussion, that Dunn was reluctant to assume more than one invasion of the West Indies by an ancestral hylid stock. Although the assumption is parsimonius in terms of historical zoogeography, it severely restricted his corollary conclusions on the evolutionary relationships of the nine taxa. He implied that the *septentrionalis* group represented the most primitive derivative of an ancestral stock; thus, *septentrionalis* (*sensu stricto*) represented a Cuban derivative, *brunnea* the Jamaican derivative, and *dominicensis* the Hispaniolan derivative. Dunn postulated that

lichenata, wilderi, and *marianae* represented derivative of *brunnea,* which diversified with respect to size while maintaining a specialized arboreal mode of reproduction. He suggested that on Hispaniola *vasta, heilprini,* and *pulchrilineata* evolved from a *dominicensis*-like ancestor. The Hispaniolan derivatives diversified with respect to size, but unlike their Jamaican counterparts, they also diversified with respect to breeding site (*i.e.,* pond and stream) within the more generalized aquatic reproductive mode.

Noble (1927) commented at some length on Dunn's proposal in his discussion of the significance of life history data in the evolution of the Amphibia. He suggested that the tadpoles of the Hispaniolan hylids seemed to represent an orthogenetic series progressively modified to life in a mountain stream, thus strengthening Dunn's argument in favor of a monophyletic origin for the group. Although, on the whole, Noble seemed to have agreed with Dunn's conclusions, he did question the high degree of parallelism involved in the evolution of the two insular faunas.

On the basis of the comparative morphological evidence presented herein, Dunn's implied monophyletic origin of the West Indian hylids is an untenable hypothesis. The four smaller species— *pulchrilineata, heilprini, marianae,* and *wilderi*—are similarly distinguished from the members of the *septentrionalis*-group and *vasta* and *lichenata,* by their size, generalized cranial structure, absence of dermal modification to the skull, and generalized pattern of throat musculature. Dunn (1926) suggested that *marianae* and *wilderi* might represent "neotenic" derivatives of a *brunnea*-like ancestor. Were this so, one would expect a striking resemblance in the pattern of osteological features between the smaller species and *brunnea.* Morphologically, *brunnea* unquestionably is distinct from *marianae* and *wilderi;* however, comparison of the two latter species suggests a close relationship between them. Myologically, *marianae* and *wilderi* differ in only three of the ten characters considered. Both are characterized by skulls with greatly reduced ossification and bluntly rounded snouts. The species share similar body proportions (Table 1), many features of soft morphology, and axial specializations such as short ilia, obtuse pelvic angles, expanded sacral diapophyses and transverse processes of nearly uniform width. Both are inhabitants of the central highlands of Jamaica, where they breed in bromeliads. *Hyla marianae* inhabits arboreal bromeliads in deciduous forest; its known altitudinal range is 122 to 895 m (Schwartz and Fowler, 1973). In contrast, the smaller species, *Hyla wilderi,* is known to inhabit both terrestrial and arboreal bromeliads in dense and scattered woodlands at elevations between 122 and 610 m (*op. cit.*).

There seems to be no evidence linking either *pulchrilineata* or *heilprini* to *marianae* and *wilderi.* Osteologically, both Hispaniolan

species are far more generalized than the Jamaican species; they are characterized by longer ilia, vertebral processes of subequal length, and more heavily ossified skulls. The resemblance of *pulchrilineata* and *heilprini* is limited to an absence of arboreal specializations in these species. Cranially, *pulchrilineata* is distinctly different from any other West Indian hylid. *Hylid heilprini* is uniquely distinguished by its dermal submental gland and specializations adapting it to life along mountain streams of Hispaniola; included among these specializations are the presence of a propollical spine, well-developed palmar and plantar webbing, and extensive development of subarticular and supernumerary tubercles.

Dunn was correct in his assessment of *septentrionalis*, *brunnea* and *dominicensis*. These three species comprise a closely related complex of moderately large frogs characterized by uniquely specialized throat musculature (differentiated intermandibularis muscle). The skulls are heavily ossified (exostosed, casqued, and co-ossified) and share many structural details in common, including presence of a dermal sphenethmoid and similar prevomerine morphology. In contrast to the specializations of the skull, the axial osteology of these three species is quite generalized. Sacral diapophysis expansion is moderate, and the transverse processes are distinctly subequal in length. The ilia of each of these species are long and the pelvic angle is obtuse.

Although it is not at once obvious, *lichenata* and *vasta* are more similar to one another in many respects than either is to the *septentrionalis* group. Both are extremely large frogs, sharing a generalized pattern of throat musculature (*i.e.*, differentiated intermandibularis muscle) and many arboreal specializations. The latter include dermal fringes along the outer margins of the fore- and hind limbs, and certain characteristics of the axial and pelvic skeleton. The ilia are somewhat shorter than those of the *septentrionalis* group and the anterior pelvic angle is acute or perpendicular, instead of obtuse. These two species are unique among the West Indian hylids in having very slightly dilated sacral diapophyses, the total width of which is greater than that of the third presacral vertebrae. Furthermore, in both *lichenata* and *vasta*, the transverse processes of the vertebrae are long and nearly uniform in length. We are not implying that these two species are closely related; there is a host of morphological differences distinguishing them. On the other hand, the structural characteristics which they share make it seem highly unlikely that either species could have been derived from the *septentrionalis* group as proposed by Dunn. The most distinctive feature of *lichenata* is its heavily casqued, co-ossified skull. Although this would seem to indicate a relationship to the *septentrionalis* group, the basic cranial architecture is distinctly different and certainly not derived from the pattern of these

frogs; furthermore, the undifferentiated intermandibularis sets it further apart from members of that group. Similarly, the vacuous, poorly ossified skull of *vasta* could only have arisen from the *septentrionalis* group by heterochronous arrestment of bone deposition, which is not commensurate with the size attained by this species.

On the basis of the accumulated evidence, there seem to be minimally six phylogenetic lines represented among the West Indian hylids—three having given rise to the four smaller species and three others ancestral to the five larger species. Of the smaller species, *marianae* and *wilderi* are the only species for which a common ancestor can be postulated. Unfortunately, at this time there is no clear evidence linking *wilderi* and *marianae* to any particular group of hylids currently known from South or Central America. Although both species are highly specialized for an arboreal mode of existence, *marianae* is the more generalized. It is larger, and possesses fewer morphological specializations than *wilderi.* Presumably, the ancestral stock was similar to *marianae*— a moderate-sized bromeliad breeder inhabiting the central highlands of Jamaica. *Hyla marianae* may represent a species closely related to the ancestral stock; the only obvious specializations of *marianae* are loss of the vocal sac and vocal slit aperture, and reduction of ilial length. In contrast, *wilderi* is clearly a more highly derived species which has retained a vocal sac and become adapted to life in smaller bromeliads. The transverse processes of the vertebrae are more uniform in width than those of *marianae,* but the ilia are somewhat longer. The skulls of the two species are nearly identical, save for the reduced ossification of *wilderi,* which can be interpreted as developmental arrestment associated with overall reduction of size in this species. Palmar and plantar webbing is reduced in *wilderi,* but retained in *marianae.* The nuptial excrescense of *marianae* is a flat horny pad, whereas that of *wilderi* is modified into a patch of keratinous spines. The larvae of both are highly specialized for their existence in bromeliads. The tadpole of *marianae* has a somewhat longer, slimmer tail with more reduced caudal fins than *wilderi,* but the larval mouth of the latter is much smaller and characterized by a distinctive ring of keratinous spines at its perimeter (Dunn, 1926).

The presence of *pulchrilineata* and *heilprini* on Hispaniola must result from two separate invasions of that island by forms unrelated to one another and the *marianae-wilderi* complex. Although nothing has been reported concerning the breeding habits and larvae of *pulchrilineata,* the species seems to represent a generalized, widespread Hispaniolan hylid. *Hyla heilprini,* on the other hand, is a specialized stream-side inhabitant whose morphological characters are highly reminiscent of the wide-spread, South American *Hyla*

albomarginata group (see Duellman, 1970, for a résumé of this species group).

The *septentrionalis* group, *vasta*, and *lichenata* seem to us to represent three distinct phylogenetic lines. Morphologically, *Hyla vasta* seems to be related to the *Hyla boans* group of Central and South America. Members of the *boans* group are large species inhabiting lowland forests, and like *vasta*, they are characterized by extensive digital webbing. They have moderately or poorly ossified skulls which are very similar in structure to that of *vasta* (see Duellman, 1970, for a résumé of this species group). The vertebral columns in this group tend to have uniform transverse processes and narrowly dilated sacral diapophyses similar to those of *vasta*. The intermandibularis muscle always bears a vast, median aponeurosis which represents a derived condition as in *vasta*. Perhaps the most intriguing similarity involves breeding behavior. Males of some members of the *boans* group (*boans*, *faber*, and *rosenbergi*) build stream-side, water-filled nests of mud or gravel in which eggs are deposited and tadpoles develop. At localities where the substrate is not amenable to these nest building habits, *boans* has been observed (Duellman, pers. com.) to utilize water-filled depressions adjacent to streams exactly as reported for *vasta* by Noble (1927).

Hyla brunnea, *dominicensis*, and *septentrionalis* form a very closely related species group characterized by their moderately large size and casqued, co-ossified crania. As a group, they are distinguished from *vasta* and *lichenata* by their differentiation of the intermandibularis to form an apical element, their obtuse pelvic angles, and generalized vertebral column structure in which the sacral diapophyses are narrower than the third presacral. These frogs seem to be highly adaptable, ecological generalists occurring over a wide elevational range (0-1500 m), in a variety of habitats. Although *brunnea* apparently breeds only in bromeliads, *septentrionalis* and *dominicensis* breed wherever standing water is available.

Of the three species, *septentrionalis* and *dominicensis* are the most closely allied and probably more closely related to an ancestral type than *brunnea*. Externally, *septentrionalis* and *dominicensis* are almost indistinguishable, differing only slightly with regard to skin tuberculation, presence of a tarsal fold and less digital webbing in *septentrionalis*. The skulls of the two species differ in only minor details involving the shape of the occipital margin, orientation of the parasphenoid alae, and articulation of the medial rami of the pterygoids. The vertebral column of *septentrionalis* tends to have transverse processes of more uniform width than *dominicensis*. *Hyla brunnea* differs distinctly from both *septentrionalis* and *dominicensis* in its cranial architecture and throat myology.

Osteologically, the *septentrionalis* group seems to be most closely

allied with *Osteocephalus,* a widespread Amazonian genus recently reviewed by Trueb and Duellman (1971). Members of this genus tend to be moderately large, lowland generalists, which are primarily found at elevations below 500 meters, but do ascend the Amazonian slopes of the Andes to elevations of 1800 meters. Like the *septentrionalis* group, members of *Osteocephalus* are characterized by broad skulls which are exostosed with a tendency towards co-ossification. The basic cranial architecture of the two groups is the same; many details are similar, including the patterns of dermal sculpturing, the pterygoids, prevomers and dermal sphenethmoids. The body proportions are similar, as is the hand and foot morphology. Two principal differences prevail between these two groups. *Osteocephalus,* like the majority of Neotropical hylids, has an undifferentiated intermandibularis muscle. Unlike most other hylids, including the *septentrionalis* group, the vocal sacs of *Osteocephalus* are paired, posterior in position and when inflated, protrude posteroventral or posterolateral to the angles of the jaws. It has been suggested that both paired vocal sacs and the development of a supplementary apical slip to the intermandibularis represent evolutionary specializations which are restricted in occurrence (Tyler, 1971). In view of the similarities of *Osteocephalus* and the *septentrionalis* group, it seems plausible to suggest that they may have had a common South American ancestor characterized by generalized throat musculature and moderately heavy cranial ossification with a tendency toward exostosis and casquing. Such an ancestor may have invaded the West Indies and evolved the derived pattern of throat musculature characteristic of the *septentrionalis* group. Subsequent isolation and evolution of an ancestral stock on Jamaica, Hispaniola, and Cuba may well have given rise to each of these three closely related species.

The extra- and intra-Antillean relationships of *lichenata* are perplexing. The species shares a great many external features and characters of axial morphology as well as some features of the vocal apparatus with *vasta,* as pointed out above. However, the cranial architecture of *lichenata* is completely unlike that of *vasta.* Furthermore, these two species are widely divergent ecologically; *lichenata* is a tree cavity dweller which breeds exclusively in bromeliads. The skull of *lichenata* is most similar to those of the genus *Trachycephalus,* a South American group which apparently is allied closely with the generalized and widespread *Osteocephalus* (Trueb, 1970). The similarities of cranial structure of *lichenata* and *Trachycephalus* are striking. Both have broad skulls which are heavily casqued and co-ossified with the same pattern of dermal sculpturing. The prevomers are similar, bearing teeth on curved elevations. The palatines are well developed, and each bears a prominent transverse ridge. The anterior pterygoid ramus has a broad max-

illary articulation which tends to extend to the midlevel of the orbit, and the parasphenoid alae are perpendicularly oriented to the long axis of the bone. The principal area of difference involves cranial ossification. The dermal roofing bones of *Trachycephalus* are heavily ossified; consequently internal suspensory and bracing elements (pterygoid and palatine) tend to be reduced (*e.g.*, no medial articulation of the pterygoid). In contrast, the dermal roofing elements of *lichenata* are less well developed and the palatine and pterygoid are robust, fully articulated bones. Furthermore, the cultriform process of the parasphenoid is exceedingly short in *lichenata* (see Trueb, 1970, for figure and osteological descriptions of *Trachycephalus*). The vertebral columns of *Trachycephalus* are characterized by subequal lengths of transverse processes and widely expanded sacral diapophyses in contrast to *lichenata*. Like the latter species, the intermandibularis muscle is undifferentiated in *Trachycephalus,* but basically similar to *Osteocephalus* and, unlike *lichenata*, the vocal sacs are paired and lateral.

In view of these conflicting suites of characters, the following conclusions can be drawn concerning the relationships of *lichenata*. 1) Because of differences in throat myology and axial morphology (see Analysis of Characters), *lichenata* cannot be derived from the *septentrionalis* group. To assume that *lichenata* may have been derived from an ancestral stock of this group would require that either the differentiated intermandibularis was independently evolved three times or that *lichenata* developed an undifferentiated intermandibularis from the specialized, differentiated muscle. Neither assumption is especially parsimonius. 2) The structure of the vocal sac apparatus in *lichenata* precludes its being derived from either *Osteocephalus* or *Trachycephalus;* however, the structure of the intermandibularis links *lichenata* more closely with these genera than to members of the *septentrionalis* group.

Apparently, *lichenata* represents a separate invasion of the West Indies by a primitive stock related to the *Osteocephalus-septentrionalis* complex. Although both the *septentrionalis* and *lichenata* ancestral lines retained the primitive subgular vocal sacs, the ancestral *septentrionalis* line was distinguished by differentiation of the intermandibularis. The resemblances of the crania of *Trachycephalus* and *lichenata* may be accounted for by a common ancestral stock and parallel evolution of the frogs which have taken up a similar arboreal mode of existence.

SYSTEMATIC ACCOUNTS

The close affinities of the members of the *septentrionalis* group and their distinctiveness from all other Neotropical hylids suggest that these frogs have undergone considerable evolution in the isolation of the Greater Antilles and should be warranted generic

recognition apart from *Hyla*. Fitzinger (1843) applied the generic name *Osteopilus* to *Trachycephalus marmoratus* Duméril and Bibron. Because *Osteopilus* is the earliest available name, the members of the *septentrionalis* group are herewith allocated to this genus.

Osteopilus Fitzinger, 1843

Osteopilus Fitzinger, 1843:30 [Type species.—*Trachycephalus marmoratus* Bibron, 1842, in Ramón de la Sagra (=*Hyla septentrionalis* Duméril and Bibron), by monotypy; *nec Hyla marmorata* (Laurenti, 1768)].

Diagnostic definition.—1) Skull slightly longer than broad, or as long as broad; 2) dermal roofing bones of skull well ossified, exostosed, and co-ossified; 3) prenasal and internasal bones absent; 4) dermal sphenethmoid present; 5) dentigerous processes of prevomers large, curved, moderately to closely positioned, and bearing a single row of teeth; 6) cultriform process of parasphenoid of normal length, terminating anteriorly just posterior to the level of the palatines; 7) vocal sac single and subgular, confined to position above interhyoideus muscle; 8) submentalis muscle moderate in size and araphic; 9) intermandibularis muscle differentiated to form supplementary apical elements; 10) fibers of intermandibularis muscle attach to posterolateral portions of submentalis muscle; 11) protractor cloacae muscle fibers extend inferiorly to ventral surface of ischial ridge; 12) tympanum large, 63-77 percent of diameter of eye; 13) finger and toe discs large and round; 14) nuptial excrescences present in breeding males; 15) inner metatarsal tubercle not modified for digging; 16) no fringes on hind or forelimbs; 17) total width of sacrum less than total width of presacral vertebra III; 18) sacral diapophyses moderately dilated; 19) transverse processes of posterior presacral vertebrae subequal in width; 20) angle between ilial shaft and preacetabular margin obtuse.

Content.—As defined here, the genus contains three known species—*Osteopilus brunneus* (Gosse), *O. dominicensis* (Tschudi), and *O. septentrionalis* (Duméril and Bibron).

Description.—Refer to section on comparative morphology.

Distribution.—The Greater Antilles, including Cuba, Jamaica, Hispaniola, Puerto Rico, and Isle of Pines, southern penisular Florida, and the Bahama islands. The genus is most common at lowland localities, although it does occur at moderate elevations (1500 m) in the highlands of Jamaica and Hispaniola.

Osteopilus brunneus (Gosse) new combination

Hyla brunnea Gosse, 1851:361 [Type not designated; type locality Savanna-la-Mar, Parish of Westmoreland, Jamaica].

Trachycephalus scutigerus Cope, 1863:45 [Holotype.—United States National Museum 6268 (now apparently lost) from "Jamaica"; Prof. C. B. Adams, collector]. Synonymy *fide* Dunn (1926:125).

Hyla septentrionalis brunnea—Barbour, 1937:81.

Diagnosis.—1) Size moderate, sexual dimorphism extreme; maximum observed snout-vent length in males 48.1 mm (mean 45.5 mm), in females, 70.0 mm (mean 60.5 mm); 2) skin on dorsum smooth except for scattered, small, round tubercles on forearm; 3) ventral skin finely granular on posterior half of abdomen; scattered, small tubercles around cloaca; 4) fingers one-fourth webbed; 5) numerous tiny supernumerary tubercles present on hand; 6) outer palmar tubercle absent; 7) nuptial excrescence of males a proliferation of small, keratinous granules; 8) tarsal fold absent; 9) toes three-quarters webbed; 10) moderate number of plantar supernumerary tubercles; 11) nostrils slightly protuberant; 12) skull longer than broad; 13) parasphenoid alae posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid narrowly separated from parasphenoid ala and with firm articulation with otic capsule; 15) anterior ramus of pterygoid articulating with maxillary at mid-level of orbit; 16) prevomerine dentigerous processes strongly curved, narrowly separated medially; 17) sacral diapophyses moderately dilated (*ca.* 41°; anterior sacral angle *ca.* 82°; posterior sacral angle *ca.* 57°); 18) interhyoideus muscle without lobes; 19) intermandibularis muscle with slender, median aponeurosis; 20) vocal sac aperture a moderate slit; 21) anterior cornu of hyoid lacking anterolateral lobe; 22) larvae with long tail, reduced caudal fins, incomplete labial disc, notched lower beak, and toothrow pattern of 1/0.

Osteopilus brunneus can be distinguished readily from the other two species in the genus by the shape of its snout, which is clearly truncate in lateral profile, terminal nostrils, smooth gular skin, finely granular abdominal skin, and absence of clearly defined transverse bars on the forearms.

Distribution.—This species is endemic to Jamaica where it is widespread at elevations below 1500 m.

Remarks.—Although *Osteopilus brunneus* has been mentioned frequently in the literature, useful accounts are few and widely scattered. Gosse (1851:361) provided notes on the natural history of the species; these were summarized and augmented by Barbour (1910:288) and Dunn (1926:125). Dunn described the call, preferred habits and sites of egg deposition, and figured the larvae and larval mouthparts (1926: Pl. 1, Fig. 2; Pl. 2, Fig. 2). The best systematic accounts are those of Barbour (*loc. cit.*) and Lynn, in Lynn and Grant (1940:19-22). Included in the latter is information on colors in preservative and in life and their variation, comments on size, variation, and statements of habits, habitat, and distribution. Lynn, in Lynn and Grant (1940:Pl. 1) also provided semidiagrammatic drawings of *brunneus*. The species was illustrated also by Noble (1931:89, Fig. 28B). Discussion and comment on the relationships of *brunneus* are available in Dunn (1926), Noble (1927),

and Duellman (1970). The most recent account of *brunneus* is provided by Schwartz and Fowler (1973). Although they acknowledged that specimens of this species are found most frequently in bromeliads, the authors also reported collecting individuals from leaves of shrubs and sides of trees (up to 2.1 m above the ground), and from the ground itself. The maximum snout-vent length they observed in male *brunneus* is 50.6 mm (mean, 45.6 mm; n=25), and in female *brunneus*, 78.5 mm (mean, 65.7 mm; n=25).

Osteopilus dominicensis (Tschudi) new combination

Hypsiboas dominicensis Tschudi, 1838:30 [Syntypes.—Museum National d'Histoire Naturelle (Paris) 4614 (four specimens) from "Saint-Dominque"; presented by M. Alexandre Ricord].

Trachycephalus dominicensis—Duméril and Bibron, 1841:540.

Trachycephalus ovatus Cope, 1863:44 [Holotype.—Museum of Comparative Zoology (Harvard) 1518 from near Jérémie, Haiti; purchased from D. F. Weinland, 1859]. Synonymy *fide* Boulenger (1882:369).

Hyla ovata—Boulenger, 1882:369 (part).

Hyla dominicensis—Boulenger, 1882:370 (part).

Hyla (Trachycephalus) ovata—Fischer, 1888:44.

Hyla (Trachycephalus) dominicensis—Meerwarth, 1901:40.

Hyla septentrionalis dominicensis—Barbour, 1937:81.

Hyla dominicensis dominicensis—Mertens, 1938:332.

Hyla dominicensis—Cochran, 1941:13.

Diagnosis.—1) Size moderately large, sexual dimorphism extreme; maximum observed snout-vent length in males 63.8 mm (mean 57.8 mm), in females 98.7 mm (mean 76.8 mm); 2) skin on dorsum smooth; 3) ventral skin of throat, abdomen, and posteroventral surfaces of thighs coarsely granular; 4) fingers one-fourth webbed; 5) numerous, tiny supernumerary tubercles present on hand; 6) outer palmar tubercle present; 7) nuptial excrescence of males a flat, keratinous pad; 8) tarsal fold absent; 9) toes three-quarters webbed; 10) few plantar supernumerary tubercles; 11) nostrils slightly protuberant; 12) skull slightly longer than broad; 13) parasphenoid alae perpendicularly oriented to longitudinal axis of skull; 14) medial ramus of pterygoid narrowly separated from parasphenoid, but not articulating with otic capsule; 15) anterior ramus of pterygoid articulating with maxillary at posterior level of orbit; 16) prevomerine dentigerous processes moderately curved, narrowly separated medially; 17) sacral diapophyses moderately dilated (*ca.* 41°; anterior sacral angle *ca.* 74°; posterior sacral angle *ca.* 65°); 18) interhyoideus muscle with postmandibular lobes; 19) intermandibularis muscle without median aponeurosis; muscles meet at tendinous raphe; 20) vocal sac aperture a small orifice; 21) anterior cornu of hyoid with anterolateral lobe; 22) larvae with short tail, extensive caudal fins, incomplete labial disc, notched lower beak, and tooth-row pattern of 2/5.

Osteopilus dominicensis can be distinguished from *O. brunneus*

by the shape of its snout, which is sloping in lateral profile, and by the coarse granularity of its gular and abdominal skin. It differs from *septentrionalis* in having more webbing between the fingers and toes, and from both *septentrionalis* and *brunneus* in the presence of a distinct outer palmar tubercle.

Distribution.—This species is endemic to Hispaniola where it is found from the coastal lowlands to moderate elevations (up to 1500 m) in the foothills and on the plateaus.

Remarks.—Although *dominicensis* was named by Tschudi (1838), the first useful description to appear was that of Duméril and Bibron (1841:540-541). Save for an illustration of the adult (Noble, 1931:89, Fig. 28 D) and the larva and larval mouthparts (Noble, 1927, Pl. IX, Fig. A), no new information was published on *dominicensis* until Mertens (1939:34-35) reported on color variation, distribution, habitat, life history, and larval characteristics. A brief account of this species, including the description of an adult female, remarks on variation in adults and a diagnostic series of illustrations was provided by Cochran (1941:13-17, Fig. 3). Lynn (1958:154-155) commented on color variation in adults and the production of irritating skin secretions by *dominicensis*, and Williams, *et. al.* (1963:315) reported phragmotic behavior in the species. Egg deposition and tadpoles were described by Noble (1927:95). Discussion of the relationships of *dominicensis* are available in Dunn (1926), Noble (1927), Myers (1950), and Duellman (1970).

Osteopilus septentrionalis (Duméril and Bibron) new combination

Trachycephalus marmoratus Duméril and Bibron, 1841:538. [Holotype.— Museum National d'Histoire Naturelle (Paris) 4612, adult female from "Cuba"; donated by Ramón de la Sagra and Henri Delaroche]. Preoccupied by *Hyla marmorata* (Laurenti, 1768:29).

Hyla septentrionalis Duméril and Bibron, 1841:538. Substitute name for *Trachycephalus marmoratus.*

Trachycephalus insulsus Cope, 1863:43 [Syntypes.—United States National Museum 12166 (adult male) and 167237 (adult female, formerly USNM 6266) from "Cuba"; collected by Felipe Poey]. Synonymy *fide* Boulenger (1882:368).

Trachycephalus wrightii Cope, 1863:45 [Holotype.—United States National Museum 5174 (adult female) from "District of Guantanamo, southeastern Cuba" (Oriente Province); collected by Charles Wright]. Synonymy *fide* Boulenger (1882:368).

Hyla schebestana Werner, 1917:36 [Holotype.—presumably destroyed in World War II, formerly Zoologisches Museum (Hamburg), no number, an adult female from "Cuba"; donated by "Herrn Apotheker Sebesta"]. Synonymy *fide* Duellman and Cromble (1970:1).

Hyla septentrionalis septentrionalis.—Barbour, 1937:81.

Hyla dominicensis septentrionalis.—Mertens, 1938:333.

Hyla dominicensis insulsa.—Mittleman, 1950:26.

Hyla dominicensis.—Peterson, Garrett, and Lantz, 1952:63.

Hyla insulsa.—Jaume, 1966:15.

Hyla septentrionalis.—Duellman and Crombie, 1970:92.1.

Diagnosis.—1) Size moderately large, sexual dimorphism extreme; average snout-vent length in males 55.3 mm, in females, 75.2 mm; 2) skin on dorsum with scattered tubercles; 3) ventral surfaces granular, tubercles absent around cloaca; 4) fingers basally webbed; 5) moderate number of low, round supernumerary tubercles present on hand; 6) outer palmar tubercle absent; 7) nuptial excrescence of males a flat, horny pad; 8) weak tarsal fold present; 9) toes about two-thirds webbed; 10) few plantary supernumerary tubercles; 11) nostrils slightly protuberant; 12) skull slightly longer than broad; 13) parasphenoid alae posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid widely separated from parasphenoid and bearing only a weak articulation with the otic capsule; 15) anterior ramus of pterygoid articulating with maxillary at posterior level of orbit; 16) prevomerine dentigerous processes moderately curved and separated medially; 17) sacral diapophyses dilated (*ca.* 57°; anterior sacral angle *ca.* 70°; posterior sacral angle *ca.* 53°); 18) interhyoideus muscle with small, supramandibular lobes; 19) intermandibularis muscle without median aponeurosis; muscles meet as tendinous raphe; 20) vocal sac aperature a small orifice; 21) anterior cornu of hyoid with anterolateral lobe; 22) larvae with moderately long tail, extensive caudal fins, incomplete labial disc, notched lower beak, and tooth-row pattern of 2/4.

Osteopilus septentrionalis is distinguished from both *dominicensis* and *brunneus* by its tuberculate dorsal skin and basal webbing between the fingers. The species differs from *brunneus* by the shape of the snout, which is sloping in lateral profile in *septentrionalis.* It differs from *brunneus* by the shape of the snout, which is sloping in lateral profile in *septentrionalis.* It differs from *dominicensis* by the absence of an outer palmar tubercle.

Distribution.—The species is widespread at low and moderate elevations throughout Cuba and on the Isle of Pines. *Osteopilus septentrionalis* also occurs on the Cayman Island (Grand Cayman, Little Cayman, and Cayman Brac) and on some of the Bahama Islands northwest of the Mayaguana Passage (Little Bahama Bank, Grand Bahama Bank, San Salvador, Rum, Crooked, and Acklin's islands). The species occurs on southern, peninsular Florida and has been introduced to Great Inagua Island and Puerto Rico.

Remarks.—A complete review of the nomenclatural history, and pertinent literature including a description of the species, its fossil record and distribution was provided by Duellman and Crombie (1970:92.1-92.4). See Cochran (1961) for black and white and color photographs of *septentrionalis.*

It is clear that *lichenata* is a highly specialized and distinctive frog which is neither closely allied to any member of the West

Indian hylid fauna nor any known representative from Central or South America. Because of its peculiar characteristics and endemism to Jamaica, we feel that this species should be accorded generic recognition.

Calyptahyla new genus

Type species.—*Trachycephalus lichenatus* Gosse, 1851.

Diagnostic definition.—1) Skull broader than long; 2) dermal roofing bones of skull well ossified, exostosed, and co-ossified; 3) prenasal and internasal bones absent; 4) dermal sphenethmoid present; 5) dentigerous processes of prevomers large, straight, narrowly separated medially and bearing a single row of teeth; 6) cultriform process of parasphenoid short, terminating anteriorly at mid-level of orbit; 7) vocal sac single and subgular; confined to position above interhyoideus muscle; 8) submentalis moderate in size and araphic; 9) intermandibularis muscle not differentiated; 10) fibers of intermandibularis muscle attach to posterolateral part of submentalis muscle; 11) protractor cloacae muscle fibers extend inferiorly to ventral surface of ischial ridge; 12) tympanum large, 68 percent or more of diameter of eye; 13) finger and toe discs large and round; 14) presence or absence of nuptial excrescences in males unknown; 15) inner metatarsal tubercle not modified for digging; 16) fringes present on hind and forelimbs; 17) total width of sacrum greater than total width of presacral vertebra III; 18) sacral diapophyses narrowly dilated; 19) transverse processes of posterior presacral vertebrae uniform in width; 20) angle between ilial shaft and preacetabular margin acute.

Content.—One species, *Trachycephalus lichenatus* Gosse.

Description.—Refer to section on comparative morphology.

Distribution.—This genus is endemic to Jamaica.

Etymology.—The generic name is derived from the Greek word *kalypto*, meaning to conceal or hide, and the Greek name *Hylas* from which the vocative *Hyla* is derived. Thus the name *Calyptahyla* (feminine) alludes to the secretive nature of this frog which has been heard to call so often in the dense woodlands of Jamaica and has been collected so infrequently.

Calyptahyla lichenata (Gosse) new combination

Hyla crucialis Harlan, 1826:64 [Type not designated; type locality "Jamaica"]. *Nomen oblitum.*

Trachycephalus lichenatus Gosse, 1851:362 [Type not designated; type locality "the summit of Bluefields Mountain, Jamaica"].

Trachycephalus anochlorus Gosse, 1851:364 [Type not designated; type locality "Jamaica"]. Synonymy *fide* Boulenger (1882:370).

Hyla lichenata.—Boulenger, 1882:370.

Diagnosis.—1) Size large, sexual dimorphism extreme; maximum observed snout-vent length in males, 92.6 mm, in females, 122 mm; 2) skin on dorsum heavily tuberculate; 3) ventral skin

granular with paracloacal folds; 4) fingers one-fourth webbed; 5) moderate number of low, round supernumerary tubercles on hand; 6) outer palmar tubercle absent; 7) presence or absence of nuptial excrescence unknown; 8) tarsal fold absent; 9) toes three-fourths webbed; 10) plantar supernumerary tubercles few in number; 11) nostrils slightly protuberant; 12) skull broader than long; 13) parasphenoid alae perpendicularly oriented to longitudinal axis of skull; 14) medial ramus of pterygoid articulating with otic capsule and distal edge of parasphenoid ala; 15) anterior ramus of pterygoid articulating with maxillary at mid-level of orbit; 16) prevomerine dentigerous processes straight, oriented at a slight angle to one another; and narrowly separated medially; 17) sacral diapophyses narrowly dilated (*ca.* 31°; anterior sacral angle *ca.* 81°; posterior sacral angle *ca.* 68°); 18) interhyoideus muscle without lobes; 19) intermandibularis muscle with slender, median aponeurosis; 20) vocal sac aperture a small orifice; 21) anterior cornu of hyoid without anterolateral lobe; 22) larva with relatively short tail, reduced caudal fins, incomplete labial disc, notched lower beak and tooth-row pattern of 1/0.

Calyptahyla lichenata can be distinguished from any other known species of Neotropical hylid by the following combination of characters: 1) single subgular vocal sac; 2) rugosely sculptured, co-ossified cranium lacking labial flanges; and 3) heavily tuberculate dorsum.

Distribution.—This species is endemic to Jamaica and widely distributed in dense forest throughout the island at low and moderate elevations.

Remarks.—Little is known about this immense casque-headed frog. The most complete account of the natural history and habits of *lichenata* was given by Dunn (1926:127-129). His descriptions were based largely on observations of Mr. E. Stuart Panton who described the call of *lichenata* and noted the preferred perch of this species in hollow trees or hollow branches of trees. The tadpole and larval mouthparts were illustrated by Dunn (1926:Pl. 1, Fig. 1; Pl. 2, Fig. 1). The adult was figured by Noble (1931:89, Fig. 28 A). The best illustrations and only complete systematic account available is that of Lynn, in Lynn and Grant (1940:22-24, Pl. II, Fig. 3). Included in the latter work are complete descriptions, comments on variation, and summaries of earlier literature. Discussion of the relationships of *Calyptahyla lichenata* may be found in Dunn (1926), Noble (1927), Myers (1950), and Duellman (1970). It should be noted that an application has been submitted to the International Commission on Zoological Nomenclature (Trueb, 1972) requesting suppression of the specific name *crucialis*, a *nomen oblitum* of 145 years. For the most recent account of this species refer to Schwartz and Fowler (1973).

The remaining five species of Greater Antillean hylids seem to be allied closely with the mainland *Hyla*. This suggests that either these frogs are more recent derivatives of mainland ancestors, or that in isolation, evolutionary change has had less dramatic effects on these phylogenetic lines than on *Osteopilus* and *Calyptahyla*. We think that until new evidence suggests otherwise, *vasta*, *marianae*, *wilderi*, *heilprini*, and *pulchrilineata* should be retained in the genus *Hyla*. A diagnostic definition of the Greater Antillean *Hyla* is provided below to distinguish members of this group from *Osteopilus* and *Calyptahyla*. For a synonymy of the genus *Hyla*, refer to Duellman (1970:173), whose arrangement has been modified only by the resurrection of *Litoria* Tschudi (Tyler, 1971).

Hyla Laurenti, 1768

Diagnostic definition.—1) Skull longer than broad, as long as broad, or broader than long; 2) dermal roofing bones poorly to moderately well ossified; not exostosed, casqued or co-ossified; 3) prenasal and internasal bones absent; 4) dermal sphenethmoid absent; 5) dentigerous processes of prevomers widely separated or not, large or small, curved or straight, usually bearing a single row of teeth; 5) cultriform process of parasphenoid of normal length, terminating anteriorly between the mid-level of the orbit and the level of the palatines; 7) if present, vocal sac single and subgular; 8) submentalis moderate in size and araphic; 9) intermandibularis not differentiated; 10) fibers of intermandibularis with or without attachment to posterolateral part of submentalis muscle; 11) protractor cloacae muscles extending inferiorly, or not, to ventral surface of ischial ridge; 12) tympanum moderately large, 50.5-61.0 percent of diameter of eye; 13) finger and toe discs large and round; 14) nuptial excrescences usually present in breeding males; 15) inner metatarsal tubercle not modified for digging; 16) no fringes on hind or forelimbs; 17) total width of sacrum more or less than total width of presacral vertebra III; 18) sacral diapophyses slightly or moderately dilated; 19) transverse processes of posterior presacral vertebrae uniform or subequal in width; 20) angle between ilial shaft and preacetabular margin varying from obtuse to acute.

Content.—As defined here, *Hyla* includes five Greater Antillean species—*Hyla vasta* Cope, *H. pulchrilineata* Cope, *H. heilprini* Noble, *H. marianae* Dunn, and *H. wilderi* Dunn.

Description.—Refer to section on comparative morphology.

Distribution.—Within the Greater Antilles, members of this genus are known only from Jamaica (*marianae* and *wilderi*) and Hispaniola (*vasta*, *pulchrilineata*, and *heilprini*).

Hyla vasta Cope

Hyla vasta Cope, 1871:219 [Holotype.—Academy of Natural Sciences (Philadelphia) 2097 from "Haiti, San Domingo"; collected by Dr. William M. Gabb].

Diagnosis.—1) Size large, sexual dimorphism extreme; maximum observed snout-vent length in males 108.8 mm (mean 96.7 mm), in females 141.9 mm (mean 136.9 mm); 2) skin on dorsum strongly tuberculate; 3) ventral skin coarsely granular; tubercles around cloaca; 4) fingers three-fourths webbed; 5) very few, indistinct supernumerary tubercles on hand; 6) outer palmar tubercle present; 7) nuptial excrescence in breeding males a flat, keratinous pad; 8) tarsal fold absent; 9) toes fully webbed; 10) plantar supernumerary tubercles absent; 11) nostrils strongly protuberant; 12) skull broader than long; 13) parasphenoid alae posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid articulating with otic capsule, widely separated from parasphenoid ala; 15) anterior ramus of pterygoid articulating with maxillary near mid-level of orbit; 16) prevomerine dentigerous processes large, slightly curved, having a moderate medial separation and a single row of teeth medially and a double row laterally; 17) sacral diapophyses narrowly dilated (*ca.* 20°; anterior sacral angle *ca.* 103°; posterior sacral angle *ca.* 57°); 18) interhyoideus muscle with postmandibular lobes; 19) intermandibularis muscle with broad, median aponeurosis; 20) vocal sac aperture a small orifice; 21) anterior cornu of hyoid without anterolateral lobe; 22) larva with short, thick tail, extensive caudal fins, complete labial disc, notched lower beak, and tooth-row pattern of 2/5.

Hyla vasta is distinguished easily from all other West Indian hylids by its size, tuberosity, and lack of a casqued, co-ossified cranium. It is unique among the Greater Antillean *Hyla* in having a sacrum which is wider than the third presacral vertebra.

Distribution.—This species is endemic to Hispaniola where it occurs from sea level to an elevation of approximately 1728 m (Schwartz, pers. com.).

Remarks.—Although Noble (1923a; 1923b) wrote two popular accounts describing his quest for the giant tree frog, *Hyla vasta*, the first noteworthy information published about this frog, its habits, habitats and life history is that of Mertens (1939:35-36). A standardized systematic account and illustrations of the species appeared in Cochran (1941:19-22, Fig. 5). Photographs of this remarkable frog in life were provided by Noble (1923a; 1923b). A drawing of the species appeared in Noble (1931:89, Fig. 28C), and the tadpole and larval mouthparts were illustrated by Noble (1927: Pl. IX, Fig. B). Discussion of the relationships of *Hyla vasta* may be found in Dunn (1926), Noble (1927), Myers (1950), and Duellman (1970).

Hyla pulchrilineata Cope

Hyla pulchrilineata Cope, 1869:163 [Holotype.—Academy of Natural Sciences (Philadelphia) 14495 from "east St. Domingo"; collected by Dr. William M. Gabb].

Diagnosis.—1) Size moderately small, some sexual dimorphism; maximum observed snout-vent length in males 39.5 mm (mean 31.6 mm), in females 42.8 mm (mean 40.1 mm); 2) skin on dorsum smooth; 3) ventral skin slightly granular on belly and thighs; no tubercles around cloaca; 4) fingers webbed basally; 5) palmar supernumerary tubercles absent; 6) two round, outer palmar tubercles present; 7) nuptial excrescence in breeding males a flat, horny pad; 8) tarsal fold absent; 9) toes two-thirds webbed; 10) few plantar supernumerary tubercles; 11) nostrils not protuberant; 12) skull longer than broad; 13) parasphenoid alae slightly posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid not articulating with otic capsule, and widely separated from parasphenoid ala; 15) anterior ramus of pterygoid articulating with maxillary at posterior level of orbit; 16) prevomerine dentigerous processes moderate sized, straight, and having a narrow medial separation and a single row of teeth; 17) sacral diapophyses dilated (*ca.* 48°; anterior sacral angle *ca.* 77°; posterior sacral angle *ca.* 55°); 18) interhyoideus muscle with small, supramandibular lobes; 19) intermandibularis muscles lacking aponeurosis, muscles meet at tendinous raphe; 20) vocal sac aperture a moderate slit; 21) anterior cornu of hyoid with anterolateral lobe; 22) larva unknown.

The absence of a dermal submental gland and prepollical spine, and the smaller size of *pulchrilineata* readily distinguish this species from *heilprini*. The characteristic dorsal pattern of stripes and the narrow head of *pulchrilineata* differentiate it from *marianae* and *wilderi*.

Distribution.—*Hyla pulchrilineata* is endemic to Hispaniola where it is widespread occurring from the coastal lowlands to an elevation of approximately 636 m on the island (Schwartz, pers. com.).

Remarks.—There is a paucity of published information on *pulchrilineata*. Although the calling sites and voice of this species are known (Schwartz, pers. com.), no tadpoles have been associated with the species. The best available systematic account of *pulchrilineata* is that provided by Cochran (1941:17-19 and Fig. 4). She included a description, comments on variation and an illustration. A photograph appeared in Noble (1923a:115).

Hyla heilprini Noble

Hyla heilprini Noble, 1923c:1 [Holotype.—American Museum of Natural History 11401, adult male, from Lo Bracita, Prov. Pacificador, Dominican Republic; collected on August 20, 1922, by G. K. Noble].

Diagnosis.—1) Size moderate, no sexual dimorphism in size noted; maximum observed snout-vent length in males 54.3 mm (mean 49.4 mm), in females 52.0 mm (mean 49.3 mm); 2) skin on dorsum smooth; 3) ventral skin coarsely granular on belly and thighs; no tubercles around cloaca; 4) fingers one-half webbed; 5) numerous small, palmar supernumerary tubercles; 6) outer palmar tubercles absent; 7) breeding males lacking a nuptial excrescence; but having an extruding prepollex and propollical spine; 8) tarsal fold absent; 9) toes fully webbed; 10) plantar supernumerary tubercles absent; 11) nostrils not protuberant; 12) skull broader than long; 13) parasphenoid alae posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid articulating with otic capsule and separated from parasphenoid; 15) anterior ramus of pterygoid articulating with maxillary at mid-level of orbit; 16) prevomerine dentigerous processes moderate sized, slightly curved, and having a wide medial separation and a single row of teeth on each; 17) sacral diapophyses dilated (*ca.* 45°; anterior sacral angle *ca.* 77°; posterior sacral angle *ca.* 58°); 18) interhyoideus muscle without separate lobes; 19) intermandibularis muscles with broad median aponeurosis; 20) vocal sac aperture an elongate slit; 21) anterior cornu of hyoid without anterolateral lobe; 22) larva with thick, short, muscular tail, extensive caudal fins, complete labial disc, notched lower beak and tooth-row pattern of 6/9.

Hyla heilprini is distinguished uniquely from all other West Indian hylids by either one of two characters—presence of a dermal submental gland and/or presence of a prepollical spine. Moreover, it is the only species having an elongate vocal slit aperture and cloacal musculature characterized by a short protractor muscle which terminates above the proximal end of the gracilis minor.

Distribution.—The species is endemic to Hispaniola, where it is widespread (occurring near torrential streams) between elevations of sea level and approximately 1728 m (Schwartz, pers. com.).

Remarks.—Noble's (1923c) original description of *Hyla heilprini* is probably the most comprehensive of the type descriptions provided for any of the Greater Antillean species. In her account of *heilprini*, Cochran (1941:22-24) offered only brief remarks on variation in addition to Noble's description, which is quoted in a large part. She also illustrated the adult (Cochran, 1941:23; Fig. 6). The larva and larval mouthparts are figured by Noble (1927:Pl. IX, Fig. C), and a photograph of the adult appeared in Noble (1923b: 119). Discussion of the relationships of *heilprini* may be found in Dunn (1926) and Noble (1927).

Hyla marianae Dunn

Hyla marianae Dunn, 1926:129 [Holotype.—Museum of Comparative Zoology (Harvard) 11122 from Spauldings, Clarendon Parish (altitude 2900 feet); collected in August, 1925, by E. R. Dunn].

Diagnosis.—1) Size moderately small, sexual dimorphism marked; maximum observed snout-vent length in males 33.1 mm (mean 28.0 mm), in females 39.6 mm (38.7 mm); 2) skin on dorsum smooth; 3) ventral skin weakly granular; tubercles present around cloaca; 4) fingers basally webbed; 5) palmar supernumerary tubercles absent; 6) outer palmar tubercle absent; 7) nuptial excrescence in breeding males a flat, horny pad; 8) tarsal fold absent; 9) toes one-third webbed; 10) few, round, plantar supernumerary tubercles present; 11) nostrils not protuberant; 12) skull as broad as long; 13) parasphenoid alae posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid articulating with otic capsule, and widely separated from parasphenoid; 15) anterior ramus of pterygoid articulating with maxillary at level of posterior half of orbit; 16) prevomerine dentigerous processes moderately small, straight, and having a wide medial separation and a single row of teeth on each; 17) sacral diapophyses moderately dilated ($ca.$ 43°; anterior sacral angle $ca.$ 75°; posterior sacral angle $ca.$ 62°); 18) interhyoideus muscle without postmandibular lobes; 19) intermandibularis muscles with slender, median aponeurosis; 20) vocal sac aperture absent; 21) anterior cornu of hyoid with anterolateral lobe; 22) larva with long tail, reduced caudal fins, complete labial disc, unnotched lower beak and toothrow pattern of 0/0.

Hyla marianae most closely resembles *H. wilderi* from which it can be distinguished by its larger size, distinct tympanum, and presence of basal webbing between the fingers and a distinct outer metatarsal tubercle on the foot. The absence of a dermal submental gland and prepollical spine differentiate this species from *heilprini*. Superficially, *marianae* might be most easily confused with *pulchrilineata* which, in contrast to *marianae*, is characterized by a pattern of narrow dorsal stripes and a head which is distinctly longer than broad.

Distribution.—This species is endemic to Jamaica where it is found in dense and scattered deciduous forest between elevations of 122 and 895 m (Schwartz and Fowler, 1973).

Remarks.—Apart from Dunn's (1926:129) brief species description and the systematic account of Lynn, in Lynn and Grant (1940: 27-28), there is virtually no published information on *marianae*. The larva and larval mouthparts were illustrated by Dunn (1926: Pl. 1, Fig. 3; Pl. 2, Fig. 3) and semidiagrammatic drawings of the adult were provided by Lynn and Grant (1940:Pl. III, Fig. 5). Dis-

cussion of the relationships of *marianae* may be found in Dunn (1926) and Noble (1927). More recently, Schwartz and Fowler (1973) provided a systematic account of this species.

Hyla wilderi Dunn

Hyla wilderi Dunn, 1925:161 [Holotype.—Museum of Comparative Zoology (Harvard) 10500, an adult male from Moneague, Saint Ann Parish, Jamaica (altitude 1200 feet); collected in March, 1925, by Dr. and Mrs. H. H. Wilder].

Hyla shrevei Taylor, 1952:1 [Holotype.—Museum of Comparative Zoology (Harvard) 26769, male, from "La Loma, Chiriquicito, Republica de Panama" (apparently in error); collected by E. R. Dunn and C. Duryea]. Synonymy *fide* Goin (1959:340).

Diagnosis.—1) Size small, little sexual dimorphism; maximum observed snout-vent length in males 27.3 mm (mean 25.8 mm), in females 28.7 mm (mean 27.3 mm); 2) skin on dorsum smooth; 3) ventral skin weakly granular; tubercules present around cloaca; 4) fingers not webbed; 5) few palmar supernumerary tubercles; 6) two outer palmar tubercles present; 7) nuptial excrescence in breeding males a group of keratinous spines; 8) tarsal fold absent; 9) toes one-fourth webbed; 10) few, low, rounded plantar supernumerary tubercles present; 11) nostrils not protuberant; 12) skull broader than long; 13) parasphenoid alae posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid not articulating with otic capsule, and widely separated from parasphenoid; 15) anterior ramus of pterygoid articulating with maxillary at posterior level of orbit; 16) prevomerine dentigerous processes small, patch-like, and having a wide medial separation and single row of teeth on each; 17) sacral diapophyses dilated (*ca.* 48°; anterior sacral angle *ca.* 80°; posterior sacral angle *ca.* 52°); 18) interhyoideus muscle without postmandibular lobes; 19) intermandibularis muscles with slender, median aponeurosis; 20) vocal sac aperture a moderate slit; 21) anterior cornu of hyoid without anterolateral lobe; 22) larva with relatively short tail, reduced caudal fins, complete labial disc with keratinous "spines" arranged around perimeter, unnotched lower beak, tooth-row pattern of 0/0.

Hyla wilderi can be distinguished from *marianae* by the smaller size, indistinct tympanum, absence of webbing between the fingers, and absence of an outer metatarsal tubercle in the former. Absence of a chin gland and prepollical spine differentiates this species from *heilprini*. The broader head and absence of dorsal stripes distinguishes *wilderi* from *pulchrilineata*.

Distribution.—This species is endemic to Jamaica where it is widely distributed in open woodlands between elevations of 122 and 610 m (Schwartz and Fowler, 1973).

Remarks.—A complete systematic account of *Hyla wilderi* is provided by Lynn, in Lynn and Grant (1940:25-26); he also illus-

trated the species (Pl. III, Fig. 4). The larva and larval mouth-parts are figured by Dunn (1926:Pl. 1, Fig. 4; Pl. 2, Fig. 4). Relationships of this species are discussed by Dunn (1926) and Noble (1927). The most recent account of *wilderi* is that of Schwartz and Fowler (1973). They reported finding individuals in both arboreal and terrestrial broemliads and observed a maximum snout-vent length in males of 27.9 mm (mean, 25.5 mm; n=25) and 29.2 mm in females (mean, 26.4 mm; n=25).

ORIGIN OF THE GREATER ANTILLEAN HYLID FAUNA

Graham (1972) summarized the paleophysiography of the Caribbean Basin and noted that there is no evidence that the Greater or Lesser Antilles either were rafted to their present positions or connected to continents in the past. In the absence of contrary evidence, he assumed that the islands have maintained their characteristic arc-configuration (extending from the Yucatan Peninsula to Venezuela) throughout the Tertiary, although the spatial relationships between individual islands may have varied considerably during middle and late Tertiary times. The variation in spatial relationships supports Williams's (1969) statement that the lowest islands of the Lesser Antilles may have been submerged several times during the Pleistocene. Graham (1972) proposed that the flora of the Antilles is derived from 1) long distance dispersal of floral elements from Yucatan-northern Central America, and 2) from northern South America. In the probable absence of any inter-island land connections among the Greater Antilles, and the absence of sustained connections among the islands of the Lesser Antilles, inter-island dispersal of most forms would then depend, at least in part, upon waif dispersal by wind and water. The relatively high frequency with which rafts of sufficient size to transport plants and small animals occur in the Caribbean has been documented by King (1962).

Among the reptiles and amphibians of the Antilles, three groups have been studied extensively; these are the hylid and leptodactylid frogs, and the anoline lizards. The extensive publications of Schwartz on leptodactylid frogs are taxonomic and are not concerned with the distributional patterns, ecology, and zoogeographic history of the group. In contrast, the studies of Williams (*e.g.,* 1969, 1972) delve into the phylogenetic relationships and zoogeographic history (particularly as it relates to inter-island dispersal, colonization, competition, coexistence, and speciation) of the numerous anoline lizards of the Antilles. In view of Williams' work especially, we are tempted to compare our zoogeographic conclusions with his. As these conclusions relate to our hypothesis, Williams states (pers. com.) that with respect to anoline lizards he

believes, ". . . that the Greater Antilles have received relatively few invaders, usually one per major group [see Williams, 1969] and that complex radiations involving considerable island interchange have occurred." He further postulates that there have been only two invasions of *Anolis*—"From two colonists—one to Puerto Rico or Hispaniola—I would derive a fauna of *ca.* 70 species. I would indeed recognize two other anoline invasions, one to provide Cuba with the two species of *Chamaeleolis* and another to provide Hispaniola with *Chamaelinorops.*" In considering Williams' statements with respect to our conclusions, there are several basic differences in the faunas under study that should be noted. First, we are dealing with amphibians, not reptiles. Although both groups can, and undeniably have, dispersed over water, the chances for successful dispersal and subsequent colonization in anurans are less than those for lizards for obvious structural and physiological reasons. Furthermore, among anurans of the Antilles (bufonids, leptodactylids, and hylids) the hylids are the least likely to be able to disperse successfully over water for reasons discussed beyond. Finally, we are dealing with a much smaller extant fauna, and have no way of estimating possible or probable extinctions if, in fact, they occurred. Given these limitations, we have attempted to construct a zoogeographic model compatible with the available paleophysiographic evidence, morphological evidence, and systematic conclusions resulting from this study.

The Greater Antillean hylids may have been derived reasonably from three sources—North America, northern Central America, and South America. As a possible source, North America merits the least consideration. Other than the occurrence of the Puerto Rican adventive, *Hyla cinerea*, no North American hylids occur in the Greater Antilles. Doubtless, this is a result of the fact that during much of the Cenozoic, peninsular Florida was submerged, thus greatly increasing the distance between the North American land mass and the Greater Antilles. *Osteopilus septentrionalis* apparently is a recent immigrant to southern peninsular Florida. The species may have rafted to Florida from nearby Cuba and/or the Bahamas, or it may have been introduced by man; both alternatives are feasible, and perhaps both occurred.

As Graham (1972) pointed out, the historical association of the Greater Antilles with Yucatan-Central America is enigmatic. Because of certain floral and faunal similarities, it is thought currently (Khudoley and Meyerhoff, 1971) that there was a connection between Cuba and northern Central America and that this connection may have been in the form of closely spaced island "stepping stones." If this is so, then frogs, like plants, may have dispersed by means of rafts to Cuba from Central America. Of those species for which related, mainland forms may be postulated, only *Hyla*

vasta and *Hyla heilprini* have related taxa occurring in Central America. We have proposed that *vasta* is related to the *Hyla boans* group. The greatest diversity of this group is in South America, although three species (*boans, crepitans,* and *rosenbergi*) range into Central America as far as eastern Panamá and southeastern Costa Rica; there is an isolated population of *Hyla crepitans* at Tela, Honduras (Duellman, 1970). Similarly, a representative of the *Hyla albomarginata* group, to which *heilprini* may be related, occurs in Central America. Of the nine species comprising this group, one species, *Hyla rufitela*, occurs in the Caribbean lowlands from east-central Nicaragua to Panamá; the remaining species are South American. Thus, it is possible to assume the existence of lines ancestral to *heilprini* and *vasta* in Central America. If these ancestral anurans did disperse from Central America into the Greater Antilles, then inter-island dispersal progressed from the Yucatan-northern Central America area to Cuba or Jamaica, and thence eastward to Hispaniola. Given this dispersal route, we might anticipate finding one or more of these or related species on Jamaica or Cuba. Although such forms are unknown, it is possible that they existed from Puerto Rico, which is inhabited by only two recently introduced hylids, *Osteopilus septentrionalis* and *Hyla cinerea*. Probably the strongest argument against this proposed route of dispersal is found in the prevailing wind and ocean currents which are generally east-west rather than west-east. Under these conditions, it is highly improbable that the frogs could have successfully rafted from Central America to the Greater Antilles. However, the possibility exists that dispersal took place during the separation of North and South America at the Atrato (Bolivar) Trough at a time when ocean currents may have been substantially different. Thus ancestral *heilprini* and *vasta* may have successfully colonized Hispaniola and been excluded from Puerto Rico either by competition or inter-island ocean currents which precluded their rafting westward from Hispaniola to Puerto Rico.

A third available alternative is that some, or all, of the Greater Antillean hylids originated in South America and rafted by way of the Lesser Antilles into the Greater Antilles. At least two facts favor this hypothesis. Of all the species for which related mainland forms can be postulated (*i.e.,* all except *marianae, wilderi,* and *pulchrilineata*), the related mainland groups are most diverse in tropical South America; this includes the *Hyla boans* group, *Hyla albomarginata* group, *Osteocephalus* and *Trachycephalus*. Furthermore, the existence of substantial rafts which originated from the Orinoco and reached Barbados and St. Vincent has been documented (King, 1962). Ocean currents are such that they would favor waif dispersal in a northward or northwestward direction throughout the West Indies and Bahama Islands. This seems to be

the simpler of the two possible hypotheses, save for the absence of any of the Greater Antillean frogs or related forms on the Lesser Antilles and Puerto Rico (except for *Osteopilus septentrionalis*, a recent adventive). Because of the small sizes of the Lesser Antillean islands and the presence of leptodactylids on these islands, we must assume that the hylids have been, for the most part, unsuccessful colonists (except for the member of the *Hyla rubra* complex as noted in the Introduction). For the present we must assume that competition has excluded this diverse group of species from Puerto Rico, although it seems unlikely. Despite the difficulties with this alternative, we favor South American origins of the Greater Antillean hylid fauna because the hypothesized dispersal routes are amenable with ocean and wind currents as we know them today, and because of the richness of the tropical South American frog fauna as contrasted with that of the Yucatan-northern Central American area.

Although not the largest island in the Greater Antilles, Hispaniola has extremely diverse habitats. If we assume a South American origin of the Greater Antillean hylid fauna, then Hispaniola is also nearer the mainland source of frogs than Jamaica, Cuba, or the Bahamas. Because of its size, relative distance from the mainland, and variety of habitats, we should expect a more diverse anuran fauna on Hispaniola than on the remaining islands. This, in fact, turns out to be the case. Hispaniola support 2 species of *Bufo* (Bufonidae), 1 species of *Leptodactylus* (Leptodactylidae), at least 42 species of *Eleutherodactylus* (Leptodactylidae), and 4 hylid species. Because of the degree of their morphological distinctiveness (see Analysis of Characters), the hylid species which occur on Hispaniola seem to represent four distinct phylogenetic lines, and therefore, four separate, successful invasions. Although there is distributional sympatry, the species differ in size and/or habitat preference so that interspecific competition would appear to be minimal or non-existent. There seems to be a co-adjustment of species pairs by size (Fig. 1) reminiscent of Schoener's Second Rule as stated by Williams (1972:57-58) in his discussion of the anoles of the West Indies. Both *Osteopilus dominicensis* and *Hyla pulchrilineata* appear to be generalists most common at lower elevations; however, *dominicensis* is about half again as large as *pulchrilineata*. *Hyla vasta* is between two and three times as large as *Hyla heilprini*; both use streams as breeding sites, although *heilprini* breed in swifter parts of the streams than *vasta*. It would seem that competition might occur between *vasta* and *dominicensis*; however, *vasta* is about one-third larger than *dominicensis*, and *dominicensis* breeds in quiet, rather than moving water.

Jamaica is much smaller than Hispaniola and, based on the suggested dispersal scheme, more distant from the mainland; thus,

we should expect it to have a lower immigration rate, and therefore, fewer species (MacArthur and Wilson, 1967:22-23). Only one species of *Bufo* (Bufonidae) occurs on Jamaica, and it is an adventive (Schwartz and Fowler, 1973). In addition to the four hylids, there are 15 species of *Eleutherodactylus* (Leptodactylidae), three of which have been introduced (*op. cit.*). Although Jamaica supports the same number of hylid species as Hispaniola, the species represent three distinct phylogenetic lines and therefore, separate invasions; one of the species (*brunneus*) is closely related to *Osteopilus dominicensis* of Hispaniola. Perhaps an ancestral stock of *Osteopilus* successfully colonized Hispaniola and subsequently Jamaica, evolving into *dominicensis* and *brunneus*, respectively. Because of the distinctiveness of *Calyptahyla lichenata* from all other Antillean anurans, we think it represents a separate invasion, as does the ancestral stock of *marianae* and *wilderi*. The hylids of Jamaica are much more restricted ecologically than those of Hispaniola, although the same kind of size differential prevails (Fig. 1). Williams *et al.* (1963) suggested that at some time in the past absence of standing water on Jamaica forced the resident treefrogs to breed in bromeliads. Regardless of the operant selective factor, these four species have adapted successfully to this limited resource. The two larger species, *brunneus* and *lichenata*, use larger bromeliads for breeding. *Calyptahyla lichenata* is about one-third larger than *Osteopilus brunneus* and frequents tree-hole cavities, a habit not observed in *brunneus*. *Hyla marianae* and *H. wilderi* are one-half to one-third the size of the larger hylids and therefore use smaller bromeliads for breeding than does *lichenata* or *brunneus*. Of the two smaller hylids, *wilderi* is smaller than *marianae*. We suggest that *wilderi* evolved from a *marianae*-like ancestor in the process of adapting to life in smaller bromeliads.

Cuba is much larger than Hispaniola and Jamaica, and has far more extensive arid to semi-arid lowlands than either. Although Cuba is somewhat farther from South America than Jamaica, it is, as pointed out, much larger and has an interesting anuran fauna relative to Jamaica and Hispaniola. Five species of *Bufo* (Bufonidae), about 24 species of *Eleutherodactylus*, and one species of *Sminthillus* (Leptodactylidae) occur on Cuba in addition to the single hylid representative. In view of its position, extensive lowland habitat, and anuran fauna, it is not surprising that Cuba (and the Isle of Pines) has only one hylid, *Osteopilus septentrionalis*. *Osteopilus septentrionalis* is very similar in habits and morphology to *O. dominicensis* of Hispaniola; this suggests that their common ancestor successfully invaded Cuba from Hispaniola. The ability of this group to colonize successfully is substantiated by the occurrence of *O. septentrionalis* in southern Florida and the Bahamas,

and by its apparent success on Great Inagua Island and Puerto Rico where it has been introduced recently.

Parenthetically we note that, except for the absence of naturally occurring hylids, Puerto Rico supports an anuran fauna about as diverse as that of Jamaica: two species of *Bufo* (Bufonidae), one *Leptodactylus,* and about 12 species of *Eleutherodactylus* (Leptodactylidae). Thus, of the anurans inhabiting the Greater Antilles, the leptodactylids seem to have been the most successful in inter-island colonization and subsequent adaptive radiation and speciation. This success may be related to the relative independence from fresh water these taxa have achieved by the evolution of specialized breeding habits—namely, the utilization of foam nests and more commonly, the direct development of young from eggs deposited in terrestrial situations. Bufonids, on the other hand, seem to have been the least successful colonists. They are more diverse on Cuba with five species, whereas only two species each occur on Hispaniola and Puerto Rico, and none occurs naturally on Jamaica (a distributional disparity which may relate, in part, to the relative abundance of lowland habitats on the various islands). At first thought, it would seem that a typical bufonid is hardier and less susceptible to the possible inequitable conditions encountered in waif dispersal than the smaller eleutherodactyline. However, larger size may inhibit bufonid dispersal; the smaller frog is more apt to find suitable protective cover (*e.g.*, bromeliads) in which to secret itself than the larger frog. Furthermore, bufonids have not developed the breeding specializations typical of their leptodactylid relatives. As a rule, bufonids (and, in particular, *Bufo*) deposit their small, pigmented eggs in rosary-like strings in ponds or other temporary fresh water sources. Thus, whereas a founding leptodactylid population might be established by overwater dispersal of terrestrial eggs, the possibility of a similar mode of dispersal in *Bufo* is negligible. The diversity of hylids in the Greater Antilles closely parallels that of the bufonids, except that the hylids have achieved their greatest diversity (at both generic and specific levels) on Jamaica and Hispaniola instead of Cuba—a fact which we believe is explained most logically by two facts: 1) Ecologically, the greatest area of Cuba is more suitable to habitation by bufonids than by hylids. 2) There have been multiple invasions of the Greater Antilles by hylids from South America and subsequent competition with the more numerous and adaptively leptodactylids.

The fact that we postulate more numerous invasions and far less speciation and inter-island dispersal than does Williams with respect to anoline lizards necessarily relates to several significant factors. Systematic study has shown the West Indian anoline lizards to be a closely related group, whereas our results reflect a great amount of morphological diversity, indicating that the Antillean hylids

represent several diverse phylogenetic stocks—a fact which is incontrovertible in our minds. Given that frogs probably are less successful in overwater dispersal than lizards, how do we account for the disparity in the number of postulated invasions? One possible explanation centers on extinction. The anoles have been extraordinarily successful in radiating into available niches (Williams, 1969, 1972) on the various islands. The question arises then, how many invasions of lizards, other than anolines, may have resulted in unsuccessful colonization because of competition with resident anoles? The apparent minimal amount of speciation of the various lines of hylids is probably related to 1) the limited number of niches available to them, and 2) competition with the more numerous and adaptively labile leptodactylids.

SUMMARY

A comparative study is undertaken of nine species of hylids inhabiting the Greater Antilles and Bahamas. Although information from the literature concerning the habits, habitats, breeding sites and larvae is included, we concentrate on morphological comparison of these frogs. Included in the morphological analysis of characters are sizes and proportions, characteristics of the skin, and features of the hands and feet. Osteological data on the cranium, vertebral column, and pelvic girdle are provided for each species, and in addition, data on throat and cloacal myology are presented.

On the basis of our findings, we conclude that the nine species, all of which were allocated heretofore to the genus *Hyla*, are best placed in more than one genus. *Hyla lichenata* has been assigned to a new genus, *Calyptahyla*, which is similar to *Trachycephalus* of South America. *Hyla septentrionalis*, *H. dominicensis*, and *H. brunnea* have been allocated to *Osteopilus* Fitzinger, 1843. These frogs differ in various myological and osteological features from *Hyla* and probably are related most closely to *Osteocephalus* of South America. The remaining five taxa are retained in the genus *Hyla*, although, with the exception of *H. marianae* and *H. wilderi*, they do not appear to be related closely to one another. *Hyla vasta* may be related to the *Hyla boans* group of South America, and *Hyla heilprini* to the *Hyla albomarginata* group, also of South America. We are unable to postulate any close mainland relative for *Hyla pulchrilineata*, or *H. marianae* and *H. wilderi* at this time.

We propose that the present hylid fauna of the Greater Antilles has been established by at least five separate invasions from the mainland. Although other possibilities are discussed, we favor a hypothetical colonization of the Greater Antilles by frogs which have dispersed northward through the Lesser Antilles from the South American mainland. In this way we account for the greater diversity of hylids of the nearest island, Hispaniola, as compared

to Jamaica and Cuba. Jamaica is far more diverse with respect to its resident hylids than Cuba which is farther from the South American mainland. By analyzing the sites and habitat preferences of the hylids residing on any given island we find an interesting conformity to the model of co-adjustment of species pairs by size applied recently to the Antillean anoles.

RESUMEN

Hemos emprendido un estudio comparativo de nueve especies de los hílidos que habitan las Bahamas, Cuba, Hispaniola, Puerto Rico y Jamaica. Aunque incluimos información sobre la literatura tocante a los hábitos, las habitaciones, los lugares de criar, y las larvas, concentramos en una comparación morfológica de estas ranas. Incluimos en el análisis morfológico de caracteres las dimensiones y proporciones, las características de la piel, y los semblantes de las manos y los pies. Proveemos datos osteológicos sobre el cráneo, la columna vertebral, y la pelvis para cada especie, y además presentamos datos de músculos de la garganta y de la cloaca.

A base de nuestras observaciones, concluimos que las nueve especies, todas las cuales se han atribuido previamente al género *Hyla*, representan más de un género. Nosotros asignamos *Hyla lichenata* a un género nuevo, *Calyptahyla*, que es similar a *Trachycephalus* de Sudamérica *Hyla septentrionalis*, *H. dominicensis* y *H. brunnea* han atribuido a *Osteopilus* Fitzinger, 1843. Estas ranas difieren substancialmente en algunos semblantes morfológicos y osteologicos de *Hyla*, y estas están emparentados probablemente más estrechamente a *Osteocephalus* de Sudamérica. Retenemos los cinco especies restantes en el género *Hyla*, aunque, con la excepción de *H. marianae* y *H. wilderi*, que no parecen estar emparentados unos con otros. Posiblemente, *Hyla vasta* este emparentada con el grupo *Hyla boans* de Sudamérica, y *Hyla heilprini* con el grupo *Hyla albomarginata* de Sudamérica también. No podemos postular ningún pariente cercano del continente para *Hyla pulchrilineata*, *H. marianae*, y *H. wilderi*.

Proponemos que la fauna corriente de los hílidos de las islas mayores de las Antillas se ha establecido por cinco invasiones del continente por lo menos. Aunque discutimos otra posibilidades, preferimos una colonización hipotética de las islas majores de las Antillas con ranas que hayan dispersado hacia el norte por las islas menores de las Antillas del continente de Sudamérica. De este modo, explicamos la diversidad mayor de los hílidos de la isla más cercano Hispaniola, comparado con Jamaica y Cuba. Jamaica es más diversa con respecto a los hílidos residentes que Cuba, que queda más lejos del continente de Sudamérica. Mediante análisis de los tamaños y las preferencias en habitaciones de los hílidos que viven

en alguna isla particular, hallamos una conformidad notable al modelo (Williams, 1972:57-58) que ha aplicado a los lagartillos del género *Anolis* de las Antillas.

LITERATURE CITED

BARBOUR, T.
1910. Notes on the herpetology of Jamaica. Bull. Mus. Comp. Zool., 52(15):273-301, pls. 1-2.
1937. Third list of Antillean reptiles and amphibians. Bull. Mus. Comp. Zool., 82(2):77-166.

BIBRON, G.
1842. *In* Ramón de la Sagra. Historia física, política y natural de la Isla de Cuba. Part 2, Historia natural [not seen].

BOCK, W. J. and C. R. SHEAR
1972. A staining method for gross dissection of vertebrate muscles. Anat. Anz. 130:222-227.

BOULENGER, G. A.
1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum, ed. 2, London, xvi + 655 pp.

CARR, A. F., JR.
1940. A contribution to the herpetology of Florida. Univ. Florida Publ., Biol. Sci. Ser., 3(1):1-118.

COCHRAN, D. M.
1941. The herpetology of Hispaniola. Bull. U.S. Natl. Mus., viii + 398 pp.
1961. Living amphibians of the world. Doubleday & Co. Inc., New York. 199 pp.

COPE, E. D.
1863. On Trachycephalus, Scaphiopus, and other Batrachia. Proc. Acad. Nat. Sci. Philadelphia. 15:43-54.
1869. Seventh contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 11:147-169.
1871. Ninth contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 23 (part 2):200-224.

DUELLMAN, W. E.
1970. The hylid frogs of Middle America. Monog. Mus. Nat. Hist., Univ. Kansas, 1:xi + 753 pp.

DUELLMAN, W. E. and R. I. CROMBIE
1970. Hyla septentrionalis. Cat. Amer. Amph. Rept., 92:1-4.

DUELLMAN, W. E. and A. SCHWARTZ
1958. Amphibians and reptiles of southern Florida. Bull. Florida State Mus., Biol. Sci., 3(5):181-324.

DUMÉRIL, A. M. C. and G. BIBRON
1841. Erpetologie generale ou histoire naturelle complete des reptiles. vol. 8. Paris, vi + 792 pp.

DUNN, E. R.
1925. A new tree-toad from Jamaica. Occas. Papers Boston Soc. Nat. Hist., 5:161-162.
1926. The frogs of Jamaica. Proc. Boston Soc. Nat. Hist., 38(4):111-130, pls. 1-2.

DU TOIT. C. A.
1955. The "tail" of *Ascaphus*: A historical resume and new histological-anatomical details. Ann. Univ. Stellenbosch. 31: A (1):1-71.

FISCHER, J. G.
    1888. Herpetologische Mitteilungen IV. Über eine Kollektion Reptilien
        und Amphibien von Hayti. Jahrb. hamb. wiss. Anstalt. 5, S. 23-45.
FITZINGER, L.
    1843. Systema reptilium. Vienna, ix + 106 pp.
GOIN, C. J.
    1959. A synonym and a homonym in the frog genus *Hyla*. Copeia, 1959
        (4):340-341.
GOSSE, P. H.
    1851. A naturalist's sojourn in Jamaica. London [not seen in entirety].
GRAHAM, A.
    1972. Some aspects of Tertiary vegetational history about the Caribbean
        Basin. Mem. I Congr. Latinoamericano Bot.:97-117.
HARLAN, R.
    1826. Descriptions of several new species of Batrachian Reptiles, with
        observations on the larvae of frogs. Amer. Jour. Sci. and Arts, 10
        (Art. 7):53-65.
JAUME, M. L.
    1966. Catalogo de los anfibios de Cuba. Mus. "Felipe Poey" Acad. Cien.
        Cuba, Trab. Divulg., 35:1-21.
KHUDOLEY, K. M. and A. A. MEYERHOFF
    1971. Paleogeography and geological history of Greater Antilles. Geol.
        Soc. Amer. Mem., 129:199 pp. [not seen].
KING, W.
    1962. The occurrence of rafts for dispersal of land animals into the West
        Indies. Quart. Jour. Florida Acad. Sci., 25(1):45-52.
LAURENTI, J. N.
    1768. Specimen medicum, exhibens synopsin Reptilium emendatum cum
        experimentis circa venena et antidota reptilium Austriacorum.
        Vienna, 214 pp., pls. 1-5.
LYNN, W. G.
    1958. Some amphibians from Haiti and a new subspecies of *Eleuthero-*
        dactylus schmidti. Herpetologica, 14:153-157.
LYNN, W. G. and C. GRANT
    1940. The herpetology of Jamaica. Bull. Inst. Jamaica, Sci. Ser., 1:1-132.
MACARTHUR, R. H. and E. O. WILSON
    1967. The theory of island biogeography. Princeton University Press,
        Princeton, New Jersey, xi + 203 pp.
MEERWARTH, H.
    1901. Die westindischen Reptilien und Batrachier des naturhistorischen
        Museums in Hamburg. Mitth. Naturh. Mus. Hamburg, 18:1-41
        [not seen].
MERTENS, R.
    1938. Amphibien und Reptilien aus Santo Domingo, gesammelt von
        Prof. Dr. H. Boker. Senckenbergiana, 20(5):332-342.
    1939. Herpetologische Ergebnisse einer Reise nach der insel Hispaniola,
        Wesindien. Abhandl. Senckenberg. Naturforsch. Gesellsch., 449:
        1-84, 10 pls.
MITTLEMAN, M. B.
    1950. Miscellaneous notes on some amphibians and reptiles from the
        southeastern United States. Herpetologica, 6(1):20-24.

MYERS, G. S.
  1950. The systematic status of *Hyla septentrionalis*, the large tree frog of the Florida Keys, the Bahamas and Cuba. Copeia, 1950(3):203-214.

NOBLE, G. K.
  1922. The phylogeny of the Salientia. I. The osteology and the thigh musculature; their bearing on classification and phylogeny. Bull. Amer. Mus. Nat. Hist., 46(1):1-87.
  1923a. In pursuit of the giant tree frog. Nat. Hist., 23(2):105-116.
  1923b. Field studies of Dominican tree frogs and their haunts. Nat. Hist., 23(2):117-121.
  1923c. Six new batrachians from the Dominican Republic. Amer. Mus. Novitates, 61:1-6.
  1927. The value of life history data in the study of the evolution of the Amphibia. Ann. New York Acad. Sci., 30:31-128, pl. 9.
  1931. The biology of the Amphibia. McGraw-Hill Book Co., Inc., New York, xiii + 577 pp.

PETERSON, H. W., R. GARRETT, and J. P. LANTZ
  1952. The mating period of the giant tree frog *Hyla dominicensis*. Herpetologica, 8(3):63.

RABB, G. B. and E. B. HAYDEN, JR.
  1957. The Van Voast-American Museum of Natural History Bahama Islands Expedition Record of the expedition and general features of the islands. Amer. Mus. Novitates, 1836:1-53.

SCHWARTZ, A.
  1968. The geckos (*Sphaerodactylus*) of the southern Bahama Islands. Ann. Carnegie Mus., 39(17):227-271.
  1973. Six new species of *Eleutherodactylus* (Anura, Leptodactylidae) from Hispaniola. Jour. Herpetology, 7(3):249-273.

SCHWARTZ, A. and D. C. FOWLER.
  1973. The Anura of Jamaica: a progress report. Studies on the Fauna of Curaçao and other Caribbean Islands, 43(142):50-142.

TAYLOR, E. H.
  1952. A new Panamanian treefrog. Breviora, (1):1-3.

TRUEB, L.
  1966. Morphology and development of the skull in the frog *Hyla septentrionalis*. Copeia, 1966(3):562-573.
  1970. The evolutionary relationships of casque-headed treefrogs with co-ossified skulls (family Hylidae). Univ. Kansas Publ., Mus. Nat. Hist., 18:547-716, pls. 1-12.
  1972. *Hyla crucialis* Harlan, 1826 (Amphibia): Proposed suppression under plenary powers. A.N.(S). 1892. Bull. Zool. Nomencl., 29(1):39-40.

TRUEB, L. and W. E. DUELLMAN
  1971. A synopsis of Neotropical hylid frogs, genus *Osteocephalus*. Occas. Papers Mus. Nat. Hist., Univ. Kansas, 1:1-47.

TSCHUDI, J. J.
  1838. Classification der Batrachier mit Berucksichtigung der fossilien Thiere dieser Abtheilung. Memb. Soc. Sci. Nat. Neuchatel, 2:1-100.

TYLER, M. J.
  1971. The phylogenetic significance of vocal sac structure in hylid frogs. Univ. Kansas Publ., Mus. Nat. Hist., 19:319-360.

VERDOORN, F.
 1945. Plants and plant science in Latin America. Frans Verdoorn, editor. Chronica Botanica Co., Waltham, Massachusetts, vol. 16: xxxvii + 381 pp.

WERNER, F.
 1917. Uber einige neue Reptilien und einin neuen Frosch des Zoologischen Museums in Hamburg. Mitt. Zool. Mus. Hamburg, 34:31-36.

WILLIAMS, E. E.
 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. Quart. Rev. Biol., 44(4):345-389.
 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. In Evolutionary Biology. Th. Dobzhansky, M. K. Hecht, and W. E. Steere Eds., Appleton-Century-Crofts, Vol. 6:47-89.

WILLIAMS, E. E., B. SHREVE, and P. S. HUMPHREY
 1963. The herpetology of the Port-au-Prince region and Gonave Island, Haiti. Parts I-II. Bull. Mus. Comp. Zool., 129(5):293-342, pls. 1-5.